

Classification and review of the brachiopod superfamily Plectambonitacea

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SYNOPSIS. All nominal plectambonitacean genera are reviewed, and 79 are accepted whilst 26 are placed in synonymy or rejected. New criteria for familial and subfamilial classification are established, in order of importance (i) the nature of the cardinal process (simple, trifold or trifold and undercut), (ii) the presence of a bema, and (iii) the presence of side septa. These result in 10 families of which 6 have between two and five subfamilies: the Family Grorudiidae and the Subfamilies Pelonomiinae, Spanodontinae, Palaeostrophomeninae and Craspedeliinae are new. Three new genera are erected, *Rurambonites*, *Jonesea* and *Cooperea*. Lectotypes are here selected of *Strophomena nubigena* and *S. aranea*, both of Salter, in Salter & Blanford 1865, and now ascribed to *Toquimia*.

INTRODUCTION AND HISTORY OF RESEARCH

The Plectambonitacea were a widespread and diverse superfamily during the Ordovician and Silurian, lingering on with a few representatives into the Devonian. They were the first brachiopods to develop the pseudopunctae so characteristic of the Order Strophomenida and were the stem group of that order, so that the Strophomenacea, Chonetacea and all the Suborder Productidina were their descendants. Over a hundred plectambonitacean genera have been named, as compared with the 61 genera in the *Treatise on Invertebrate Paleontology* (Williams 1965), and since so many genera, both old and new, have been erected without adequate comparison with their closest relatives, the time now seems ripe for a complete review of the entire superfamily. We have also reviewed all the families and subfamilies and tried to compile a classification built on consistent principles, with the varied form of the cardinal process taking first precedence over other features such as the possession or absence of bema or side septa, which are themselves considered more important than the possession of a platform or the valve shape and outline, which we consider of generic rather than familial importance. Ornament is so variable within the family that it seems of specific importance rather than being the basis of genera, and there is also surprising variability in other features such as the presence or absence of a pedicle valve median septum and the shape and form of the muscle fields and their bounding ridges. However, our newly defined criteria for classification appear to recognize a real evolutionary strategy, and we have completed the task with a much clearer picture of the superfamily as a whole. We have diagnosed each family, subfamily and genus, concentrating in each case only on those features which distinguish it from its close relatives and trying not to include details which are common to the group as a whole or of only specific importance within the genus.

Because so much earlier literature is obscure or neglected, and because the library facilities and collections at the British Museum (Natural History) are so good, we have also tried to list all the described species of the superfamily, over 600 in number, and to assign them to an appropriate genus, but this task is made more difficult because of the lack of adequate illustrations in so many of the original descriptions. In our opinion there is no point in erecting any further new species of Plectambonitacea unless the brachial valve interior is

properly figured; when only the mould of a valve is available in the rock, then a latex cast should be made and figured as well.

Although individual genera and species of Plectambonitacea were erected and discussed during the nineteenth and early twentieth centuries, it was not until the monograph by Jones (1928) that a survey of the group as a whole was made. Jones worked mainly on Caradoc, Ashgill and Llandovery forms and erected the Subfamily Plectambonitinae and the key genus *Sowerbyella*, as well as *Leptelloidea* and *Chonetoidea*. His study laid the foundations for subsequent discussion of the Plectambonitacea as separate from the Strophomenacea and Chonetacea. This work was followed soon by a penetrating series of papers by Öpik (1930, 1932, 1933) whose excellent illustrations and descriptions of species, particularly those from the Lower Ordovician of Estonia, were amongst the best works on brachiopods of any age or groups for their time. North American early and middle Ordovician forms, including many new genera, were published by G. A. Cooper (particularly in Ulrich & Cooper 1938 and in Cooper 1956), and all the genera erected before about 1964 were extensively reviewed in the *Treatise on Invertebrate Paleontology* (Williams 1965). Williams also assessed and revised the familial and subfamilial classification, and his compilation has formed the basis for all subsequent work. Havlíček too made valuable contributions in the substantial revision, including many new taxa, of the important Bohemian area (e.g. 1967) and indeed of the whole Mediterranean region (e.g. 1971 on

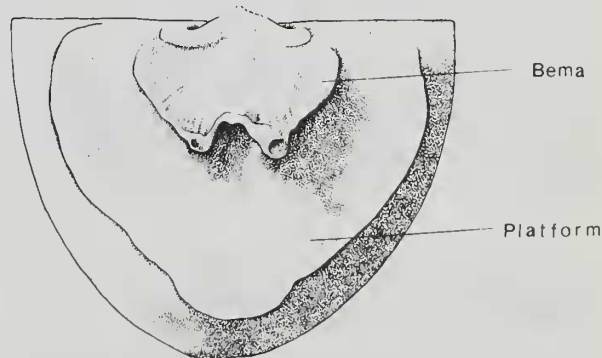


Fig. 1 Brachial valve of *Leangella scissa* (Davidson) illustrating the difference between a bema (which originates close to the anterior end of the socket plates) and a platform (which originates laterally to the structures surrounding the cardinal process).

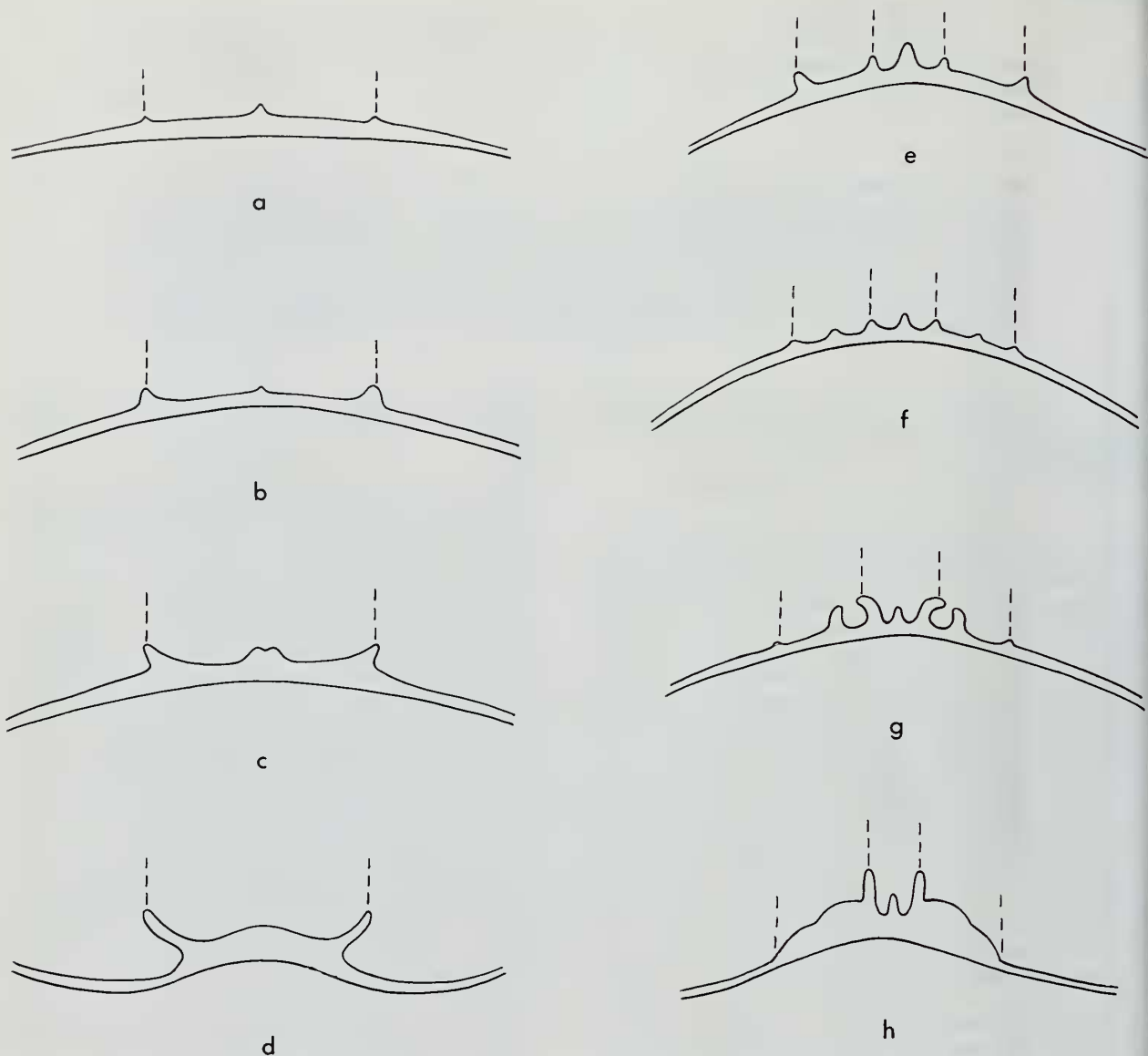


Fig. 2 Cross-section through various brachial valves to illustrate the different types of bema. The dotted lines indicate the limits of the bema, a-d are entire and e-h are divided; c and d are elevated; g and h illustrate the more extreme modifications. a, *Aegiria*; b, *Rurambonites*; c, *Leangella*; d, *Xenambonites*; e, *Bilobia*; f, *Anisopleurella*; g, *Eoplectodonta*; h, *Bimuria*.

Morocco), and Cocks (1970) revised the Silurian species of the superfamily. Many plectambonitacean species and genera have been erected or revised in other papers and monographs (see the references at the end of this work), but no revision of the group as a whole has been published since Williams (1965).

MORPHOLOGICAL TERMINOLOGY

In general we follow the nomenclature used by Williams (*in Williams et al.* 1965), but the following terms need further elucidation.

Bema: An elevated pad of secondary shell material in the brachial valve originating from or close to the anterior end of

the socket ridges or plates (Fig. 1). It may be divided into several types:

- a) entire (e.g. Figs 2a-d), divided (e.g. Figs 2e-h), or bilobed (e.g. Fig. 1)
- b) elevated (e.g. Figs 2c, d) or not elevated (e.g. Fig. 2a)

Cardinal process: The brachial valve attachment area for the diductor muscles. In the Plectambonitacea it is usually trifold (when viewed from the posterior), but may be a simple central ridge. The type of cardinal process may be divided into two main groups:

- a) simple, or not undercut, in which the central lobe is connected anteriorly to the median part of the valve floor (the notothyrial platform), often with a myophragm (e.g. Fig. 3g)
- b) undercut, in which there is no anterior support for the central lobe (e.g. Fig. 4a)

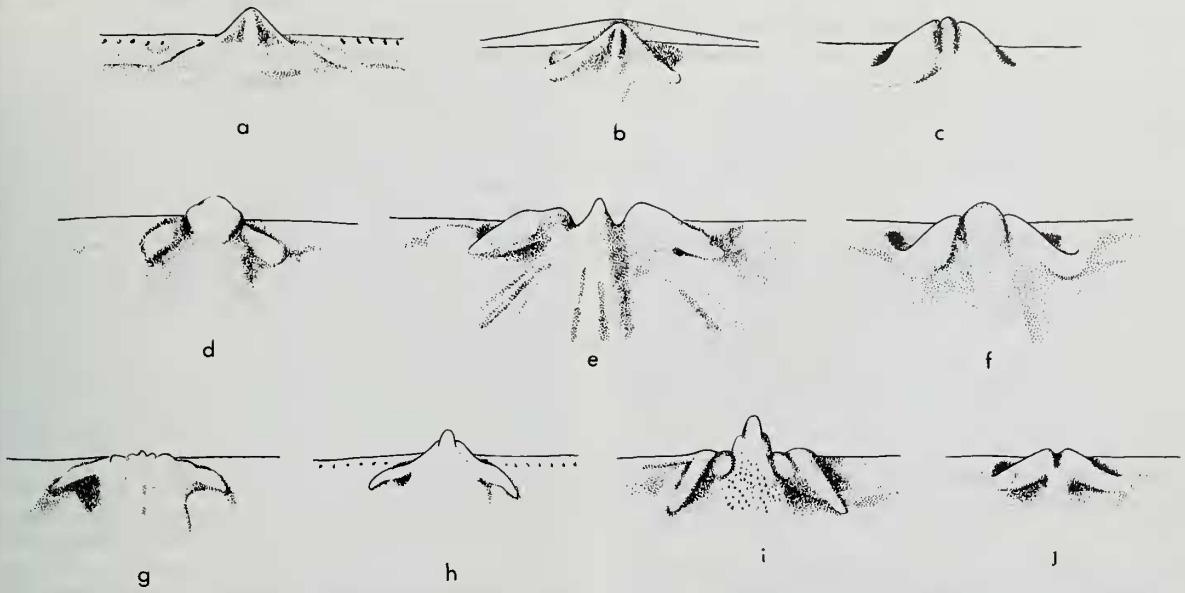


Fig. 3 Different types of cardinal process within the Plectambonitacea. a, simple, not undercut, projecting posteriorly from hinge line, *Ingria nefedyevi* (Eichwald), $\times 10$ (after Öpik 1932: pl. 6, fig. 32); b, simple, not undercut, not projecting posteriorly from hinge line, *Ahtiella baltica* Öpik, $\times 6$ (after Öpik 1933: pl. 4, fig. 6); c, simple, not undercut, *Spanodonta hoskingiae* Prendergast, $\times 6$ (from BC 10605); d, trifid, not undercut, *Toquimia kirki* Ulrich & Cooper, $\times 6$ (after Cooper 1956: pl. 164, fig. 13); e, simple, not undercut, *Bimuria superba* Cooper, $\times 6$ (from BC 7270); f, simple, not undercut and merging anteriorly with the posterior end of the double septa, *Isophragma ricevillense* Cooper, $\times 12$ (from BC 7211); g, simple, not undercut, *Leptellina tennesseensis* Ulrich & Cooper, $\times 6$ (from BB 1228); h, trifid, not undercut, *Rurambonites ruralis* (Reed), $\times 6$ (from BC 7204); i, trifid, not undercut, *Leptelloidea leptelloides* (Bekker), $\times 6$ (from B 5169); j, simple, not undercut, *Lepiella (Petroria) rugosa* (Wilson), $\times 6$ (from Cooper 1956: pl. 221, fig. 33).

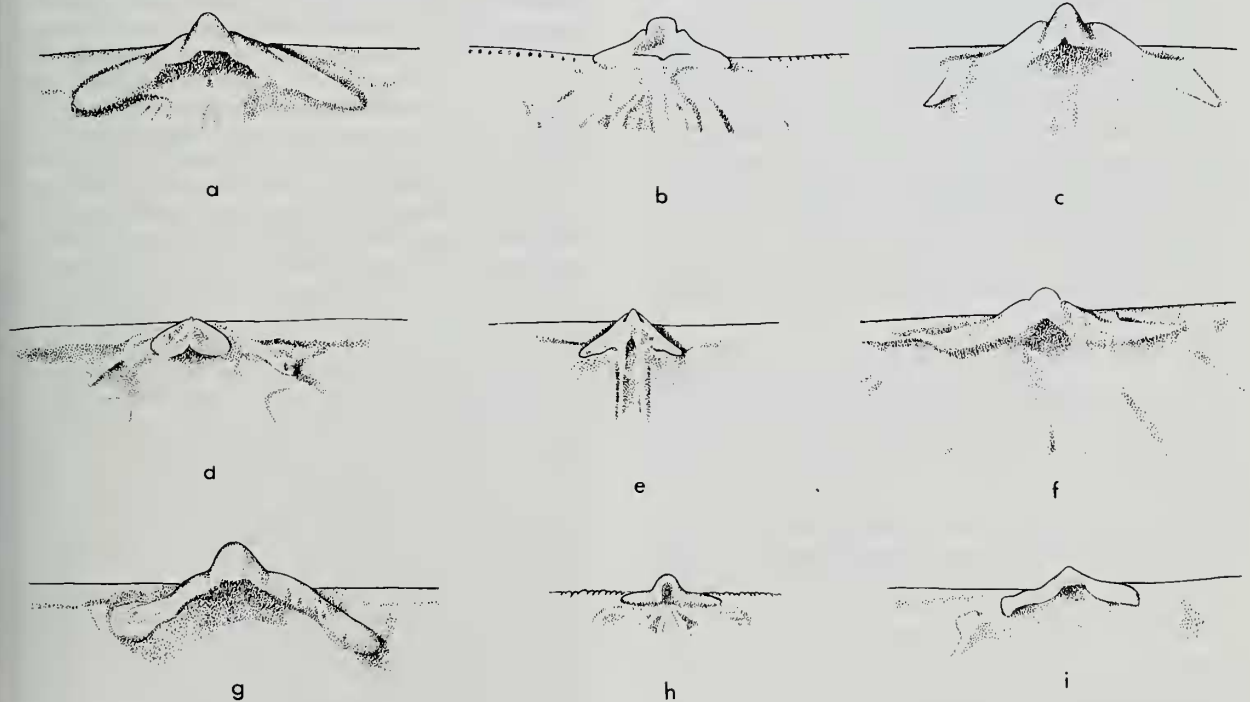


Fig. 4 Different types of cardinal process within the Plectambonitacea; all are trifid and undercut. a, *Sowerbyella eximia* Cooper, $\times 10$ (after Cooper 1956: pl. 204, fig. 32); b, *Eoplectodonta duvalii* (Davidson), $\times 6$ (from BB 31837); c, *Sowerbyella liliifera* Öpik, $\times 12$ (from BB 5149); d, *Ptychoglyptus virginianensis* Cooper, $\times 6$ (from BC 10316); e, *Gunningblandella resupinata* Percival, $\times 5$ (after Percival 1979: fig. 9.7); f, *Anisopleurella tricostellata* Cooper, $\times 25$ (from BB 32855); g, *Aegiria (Aegiria) aquila* (Barrande), $\times 25$ (from BB 33341); h, *Dalejodiscus comitans* (Barrande), $\times 7$ (after Havlíček 1967: pl. 7, fig. 9); i, *Kassinella* sp., $\times 12$ (from NIGP 101835).

Clavicular plates: Term used for structures in the brachial valve homologous to socket plates, but when there are no corresponding teeth in the pedicle valve (e.g. *Eoplectodonta*).

Dental plates: Plates in the pedicle valve going from the hinge line to the valve floor and supporting the teeth.

Denticles: Small elongate teeth distributed along the hinge line.

Median septum: Longitudinal septum in the centre of either valve. A few plectambonitaceans have a 'double' median septum consisting of a central raised area in the brachial valve with a less conspicuous median trough (e.g. Fig. 23, p. 91).

Muscle bounding ridges: Curved elevated structures in either valve bounding the muscle field laterally and/or anteriorly. In the brachial valve the muscle bounding ridges may form the edge of the bema (e.g. Fig. 94, p. 124).

Myophragm: Median raised area in either valve between muscle scars, but not extending beyond them (e.g. Fig. 37b, p. 96).

Notothyrial platform: Median thickening of brachial valve floor immediately anterior of the cardinal process.

Papillae: Distinctive small elevations on the interior of either valve, usually sub-circular: although they may coincide with the prolongation of a pseudopuncta, this is not always so, and they are usually larger than a pseudopuncta.

Peripheral rim: Raised rim near the anterolateral margin of either valve. It may be continuous as a small ridge (e.g. Fig. 75, p. 115) or discontinuous and indicated only by prominent papillae or septules (e.g. Fig. 116, p. 129).

Platform: Brachial valve structure originating near the alae (as opposed to a bema which originates at or near the socket plates). The platform (Fig. 1) may or may not be elevated from the valve floor, and may or may not be continuous.

Septules: Small elongated structures in either valve, sometimes merely elongated papillae, sometimes nearly approaching side septa in size (e.g. Fig. 95, p. 125).

Side septa: Paired brachial valve septa which may or may not be confined to the bema (some other workers have used the term 'anderidia').

Socket plates or ridges: Paired brachial valve structures attached to the hinge line and arising from near the notothyrial platform (their function varied: sometimes they were used to mesh with the teeth, sometimes they may have provided support for the posterior part of the brachiophore; see also 'clavicular plates').

Tubercles: We restrict the term within the Plectambonitacea to paired posterolateral protruberances within the pedicle valve of some genera (e.g. Fig. 114, p. 129).

FUNCTIONAL MORPHOLOGY AND EVOLUTION

It is probable that the earliest plectambonitaceans, like their orthide ancestors, had a functional pedicle and were simply attached to a variety of substrates. Their feeding mechanisms

and gape would have been typical of other brachiopods, with a relatively simple lophophore. Brunton (1972) has elegantly reconstructed the lophophore and possible water current system for a generalized chonetacean with small side septa (sometimes termed anderidia) which shows a lobed trochlophore with a single series of filaments rather than the more complex double filaments seen in most living brachiopods today. Such chonetaceans have a very similar general valve morphology to many early plectambonitaceans, such as *Taffia*, and we therefore think it likely that most primitive plectambonitaceans would have had a comparable lophophore. As with many brachiopods today, the dorsal valve simply opened very widely and stayed open without movement for feeding and respiratory purposes.

However, the interpretation of the functional morphology of the many plectambonitaceans with a variety of more substantial brachial valve structures, such as bema, side septa and platforms, is far less easy. No living articulate brachiopod has such a relatively small space between the valves, and when a very incurved plectambonitacean such as *Eoplectodonta* had its valves shut, there was very little room between them (Cocks 1970: fig. 4). In addition, the muscle scars of most plectambonitaceans appear to have been much larger than other brachiopods of comparable size. These facts led Cocks (1970) to postulate that in some advanced plectambonitaceans such as *Eoplectodonta* the flow of water over the lophophore must have been very strong whenever the valves opened or closed, and that such valve movement could have played a major part in respiration and feeding, perhaps leading to their replacing the ciliary beat as the prime method of water circulation within the shells. Such a change in function may even have led the lophophore to degenerate in size. Since then, the subject of 'flapping valves' in brachiopods has received more attention, with, for example, Cowen (1975) demonstrating that for some coral-shaped richthofeniids, it was probably the method employed (as opposed to contrary, but to our minds less compelling, views expressed by some other workers). Hurst (1975: 63) has also discussed the feeding and lophophore arrangement in *Eoplectodonta*, and concluded that the flapping mechanism for feeding was unlikely because (a) filtered and unfiltered water would have been mixed in the same channel, (b) no modern brachiopod does it, and (c) it runs against the general trend of brachiopods for the lophophore to have been reduced in size. From further experience, we would now agree with Hurst's third point, and consider it improbable that the lophophore would have degenerated in size; however, none of his other arguments against the use of valve flapping for water circulation seem strong when compared with the arguments originally presented by Cocks (1970: 149–150). Hurst agreed that the strong muscles were probably developed initially to return to a living position valves which had been overturned, but, once having developed such strength, it seems difficult to believe that it was not also used to enhance the water flow between the two valves in incurved genera of the superfamily. It is also difficult to account for the function of platforms, since, as the cross-section through *Leangella* shows (Cocks 1970: fig. 4a), there would have been no room for a lophophore anterior of the platform once the valves were shut. The lophophore was probably attached to the posterior edge of the platform anteriorly, so that when the valves were closed the lophophore was accommodated between the platform and the bema edge. Living *Argyrotheca* has comparable restricted brachial cavities, with septa crossing the cavity when the two shells are closed.

The life positions of various genera also varied greatly. Many genera, particularly the earlier and more primitive ones, had functional pedicles, and these presumably lived umbones downwards and with their shells either vertical or lightly inclined. However, many of the more advanced genera, in particular the later Sowerbyellidae such as *Eoplecodonta*, did not have functional pedicles in adult life, and thus can only have lived freely on the sea floor, obviously with their concave sides upwards to keep the valve gape clear of the substrate.

Ultrastructural studies (Brunton 1972) have shown that the plectambonitacean primary layer is similar to both chonetaceans and strophomenaceans. However, the secondary shell layer differs within the Plectambonitacea: the sowerbyellids have standard fibrous secondary shell structure, but *Aegiromena*, *Jonesea* and *Sericoidea* display a modified shell structure termed 'transitional fibrous' by Brunton (1972: 18). The earliest chonetaceans also show an ultrastructure comparable (but not identical) with the Aegiromeninae. However, given the conservative nature of the cardinal process throughout the phylum as a whole, it seems to us more probable that the chances that the development of the strophomenacean bifid cardinal process was a monophyletic evolutionary event seem higher than that of the pattern of shell structure repeating itself. Therefore, we consider it most probable that the strophomenaceans developed in the early Ordovician (Llanvirn) from the Plectambonitacea by a change from a simple to a bifid cardinal process, and that the chonetaceans developed in the late Ordovician (Ashgill) from the strophomenaceans (either rafinesquinids or pholidostrophiids) by the simple acquisition of hinge line spines and with no change in the character of the cardinal process. Thus we do not consider the Plectambonitacea as the immediate ancestors of the Chonetacea.

The pattern of evolution of the superfamily is set out in Fig. 5. It assumes that the most important character is the development of the cardinal process from simple to trifold and from trifold to undercut. Each of these three major cardinal process stages also developed bema and side septa to give the pattern of families which we have identified. The oldest plectambonitaceans are of Tremadoc age and are essentially indistinguishable from their orthide (probably billingsellacean) ancestors except by their pseudopunctate shell. The only definite plectambonitacean of late Tremadoc age is *Plectella* (Plectambonitidae); *Leptella? exigua* is also of certain late Tremadoc age although there are no interiors known of it. There is also uncertainty about the affinities of the undoubtedly late Tremadoc genus *Akelina* (see below p. 88). True *Leptella* (Taffiidae) are known from the Lower Arenig, and we have indicated the Taffiidae as the ancestral plectambonitaceans in our evolutionary diagram because we regard the absence of side septa (as in the Taffiidae) as representing a more primitive state than their presence (as in the Plectambonitidae). The great period of plectambonitacean diversification occurred in Llanvirn times, which is also the age of the oldest known strophomenacean, the presumed descendant of one of the plectambonitacean stocks; perhaps one related to some leptellinid like *Apatomorpha* or *Toquimia*. In fact eight out of the ten plectambonitacean families had evolved by the end of the Llanvirn. From that time until their extinction in the early middle Devonian, the morphological changes appear to have been far less radical in character.

CRITERIA FOR CLASSIFICATION

After studying specimens and/or photographs of all the type species of all the plectambonitacean genera, we conclude that the brachial valve characters are those upon which the most suitable family and subfamily classification can be built. In particular, the nature of the cardinal process enables us to identify a more primitive group which shares with its parent orthides a simple cardinal process which is supported directly anteriorly by a swollen notothyrial platform. This simple cardinal process was subsequently joined by a pair of lateral processes to form the normal trifid cardinal process typical of most plectambonitids. A more advanced group of genera consists of those in which all the support comes from the lateral structures joined to the bases of the socket plates or ridges, leaving a space immediately anterior to the cardinal process; this type we term as having an undercut cardinal process. Some authors in the past have used a morphological term for this space in front of the cardinal process, for example 'Schlössgrube' (Öpik 1933) or 'alveolus' (Muir-Wood 1962); however, we feel it misleading to use positive terms for negative features, and prefer to think of this space as a gap between structures, rather than as a structure in its own right, and so a special name is not used in this paper.

However, despite the generally conservative nature of the cardinal process, on some occasions it does not appear to have developed at all, for example in *Taffia* it is generally absent, although appearing occasionally within a population (Neuman 1977), and also in *Leptella*, where it is not known at all. Nevertheless, the general morphology of *Leptella* is extremely close to some other taffiids and thus the genus has been placed in the Taffiidae with some confidence. Another difficult decision is to determine whether or not the trifid cardinal process evolved once or twice. In particular, on Fig. 5 the Syndielasmatidae are shown as arising from the Plectambonitidae because the morphologies of the two families are so close. However, although we have chosen this as the most likely alternative, it may have been that the trifid cardinal process only evolved once and the Syndielasmatidae (with their side septa and no bema) may have been derived through a cryptic route unrepresented by known fossils. Apart from the possible exception of the Syndielasmatidae the evolution of the cardinal process appears to have taken place in unique and irreversible steps.

The second prime criterion for familial classification is the presence or absence of a bema. This structure has often in the past been confused with or taken as a homologue of a platform, but they differ fundamentally in that the bema originates at or very near the anterolateral ends of the socket plates or ridges, whilst the platform originates laterally from these sites, along the hinge line and often well into the alae. *Leangella*, for example, possesses both bema and platform, and Fig. 1 shows both of them extending well into the alae. The definition and consistent recognition of the bema has caused confusion and lack of consistency among previous authors. For example, Cooper sometimes used 'visceral disk' when he was describing a platform (e.g. in *Leptellina bella*; 1956: 749) and sometimes when he was describing a bema (e.g. in *Bilobia virginensis*; 1956: 762); Williams used the term 'lophophore platform' for a platform (e.g. in *Leptellina rhacta*; 1963: 164) and sometimes for a bema (e.g. in *Leangella* cf. *hamari*; 1963: 172), and Havlíček, although for the most

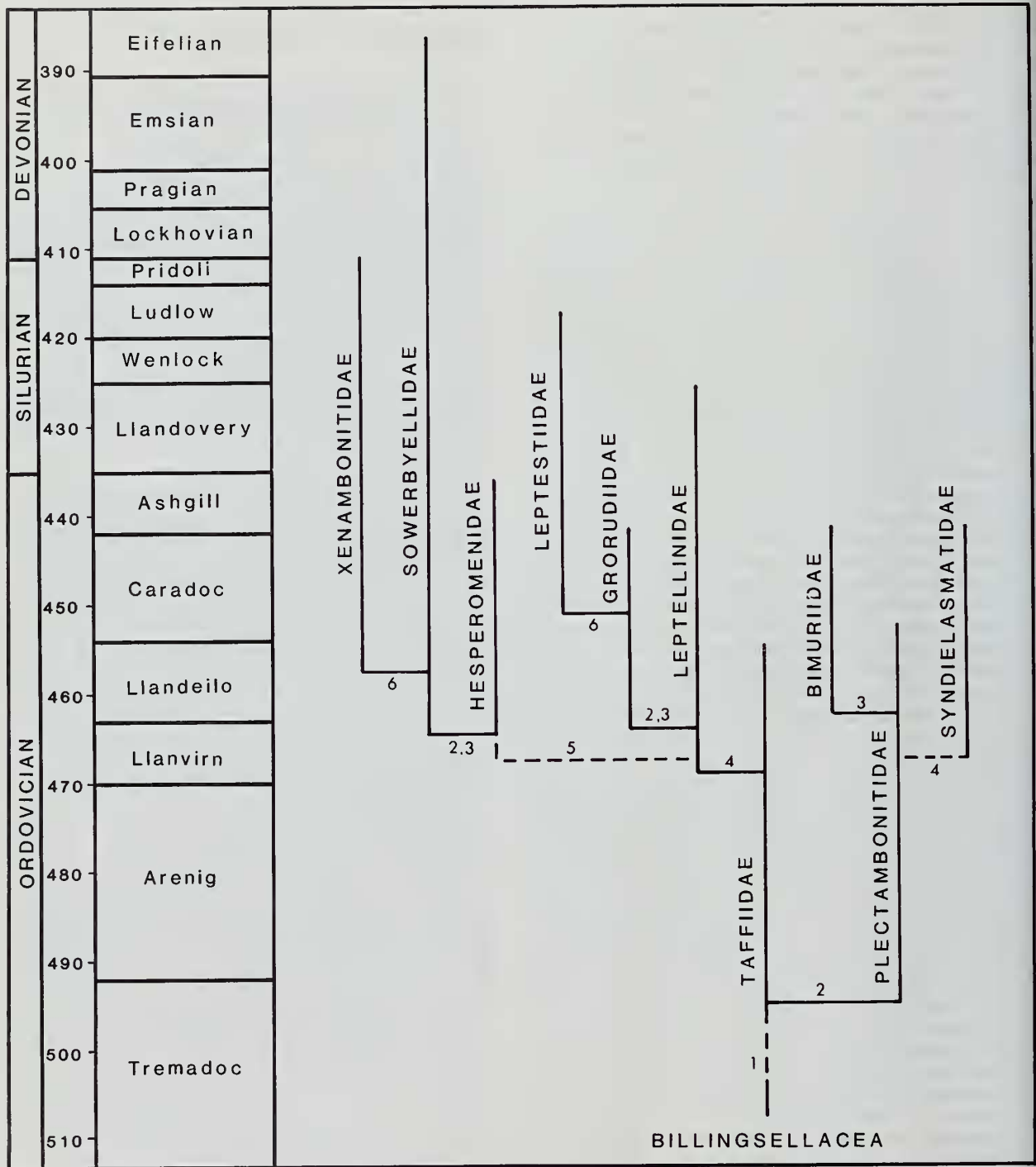


Fig. 5 Range chart and phylogeny of the families of the Plectambonitacea. The numbers indicate the acquisition or loss of critical characters as follows: 1. acquisition of pseudopunctae; 2. acquisition of side septa; 3. acquisition of bema; 4. acquisition of trifid cardinal process; 5. acquisition of undercut cardinal process; 6. loss of side septa.

part he consistently termed the bema a 'visceral field' (e.g. in *Anisopleurella ovalifera*; 1967: 65), he sometimes called it a 'visceral platform' (e.g. in *Leptestiina prantli*; 1967: 30), and often called the platform the 'diaphragma' (e.g. in *Tufoleptina tufogena*; 1967: 34). However, in a few cases, Havlíček confused 'diaphragma' with 'visceral platform'. For example,

there is a platform in *Anoptambonites moneta* (Havlíček 1967: 36), which was called by him a 'visceral platform'. We have found the presence or absence of a platform to be a less fundamentally important character in classification, and useful only in identifying and grouping subfamilies and sometimes only in the separation of two otherwise

closely-related genera (for example *Titanambonites* and *Shimia*). The third character which we have used on our familial separations has been the presence or absence of side septa in the brachial valve, which has been useful in some cases, but appears to have been less fundamental in strategic evolutionary importance and also to have occurred on several different occasions (Fig. 5).

Therefore, using the three stages of development of the cardinal process and the presence or absence of a bema and side septa, there are twelve possible permutations and combinations, and we have identified plectambonitaceans belonging to ten of them, as follows:

- 1 Cardinal process simple, no bema, with side septa, e.g. *Plectambonites* (Fig. 12, p. 87).
- 2 Cardinal process simple, no bema, no side septa, e.g. *Borua* (Fig. 32, p. 95).
- 3 Cardinal process simple, with bema, with side septa, e.g. *Bimuria* (Fig. 46, p. 101).
- 4 Cardinal process trifid, no bema, with side septa, e.g. *Syndielasma*.
- 5 Cardinal process trifid, no bema, no side septa, e.g. *Leptellina* (Fig. 49, p. 105).
- 6 Cardinal process trifid, with bema, no side septa, e.g. *Leptestia* (Fig. 78, p. 118).
- 7 Cardinal process trifid, with bema, with side septa, e.g. *Tetraodontella* (Fig. 68, p. 113).
- 8 Cardinal process undercut, with bema, no side septa, e.g. *Aegiria* (Fig. 94, p. 124).
- 9 Cardinal process undercut, no bema, no side septa, e.g. *Anoptambonites* (Fig. 107, p. 127).
- 10 Cardinal process undercut, with bema, with side septa, e.g. *Eoplectodonta* (Fig. 137, p. 136).

This forms the basis for the ten families recognized in this paper. There are more than enough familial-rank names already erected by previous workers to suffice for this classification, but application of our new concepts for family classification has meant that the definition and scope of the family grouping has had to be changed in all cases, as becomes clear in the systematic section below; and in addition it has been necessary to erect one new familial and four new subfamilial names.

We have found that the pedicle valves in the Plectambonitacea are of much simpler construction than the brachial valves, and thus display a great deal of homoeomorphy, and so are not useful for familial or subfamilial classification, although in a few cases the pedicle valve morphologies have been useful in separating closely related genera.

One of the biggest problems in identifying and classifying plectambonitacean genera and species is the very large amount of variation seen in some populations and between populations. An example is the development of a short median septum in the pedicle valve of *Bilobia hemisphaerica* Cooper, which is present in most specimens of the type population (Cooper 1956: pl. 193, figs 29, 30), scarcely visible in some specimens (Cooper 1956: pl. 193, fig. 28) and absent in others (Cooper 1956: pl. 193, fig. 27). There are comparable occurrences in *Bilobia etheridgei* (Davidson), in which the median septum usually occurs (Mitchell 1977: pl. 14, figs 17, 20), but is sometimes absent (Mitchell 1977: pl. 14, fig. 24) and also in *Jonesea grayi* (Davidson), in which the septum also sometimes occurs (Cocks 1970: pl. 17, fig. 13) and is sometimes absent (Cocks 1970: pl. 17, fig. 11). These examples bring into question the true generic differentiation between, for example, *Leangella*, which has no pedicle valve

median septum, and *Diambonia*, which has virtually identical morphology to *Leangella* except for the development of a pedicle valve median septum, and thus we follow Mitchell (1977: 78) in placing *Diambonia* within the synonymy of *Leangella*. In the same way, we have found the morphology and proportion of the muscle scars within the pedicle valve to be extremely variable, and of value at most in only specific differentiation, and thus genera such as *Benignites*, which is only differentiated from *Leptellina* in 'having a slender adductor scar narrowing to the front of the ventral muscle field (but never surrounded by diductors)' (Havlíček 1976: 368), are not recognized as valid in this paper. The only exception we have found is the development of distinctive tubercles in the posterolateral parts of the pedicle valve, which appear to differentiate consistently the genera *Kassinella*, *Trimurellina* and *Jonesea* from their relatives within the families Hesperomenidae and Xenambonitidae.

The basic shell form, including the development of resupination, geniculation or rugation, can be of importance at the generic level, but these shapes have all arisen several times polyphyletically, and thus do not appear to be useful in distinguishing familial groupings or subfamilial groupings by themselves. For example, resupination occurs in the very unrelated genera *Ahtiella* and *Gunningblandella*, and geniculation in *Craspedelia* and *Xenambonites*. Two different types of rugation can be developed, one which is continuous (like the strophomenid *Leptaena*) and which is developed in many plectambonitacean genera near the alae, and over the whole shell surface in *Reinversella*, and a second type which is discontinuous (like the stropheodontid *Cymostrophia*) which is seen in the Plectambonitacea in the unrelated *Ptychoglyptus* and *Rugosowerbyella*.

Thus the most important characteristics for the families we recognize may be tabulated as follows:

	Cardinal Process	Bema	Side Septa
Plectambonitidae	simple	No	Yes
Taffiidae	simple	No	No
Bimuriidae	simple	Yes	Yes
Syndielasmatidae	trifid	No	Yes
Leptellinidae	trifid	No	No
Groruriidae	trifid	Yes	Yes
Leptestiidae	trifid	Yes	No
Xenambonitidae	undercut	Yes	No
Hesperomenidae	undercut	No	No
Sowerbyellidae	undercut	Yes*	Yes

* A few Sowerbyellidae lack a bema (see below under individual genera), but we consider that their relationships with other members of the family are so close that the bema appears to have been secondarily lost in those cases.

SYSTEMATIC PALAEOONTOLOGY

In this section we review each plectambonitacean genus in turn and include a simple diagnosis which merely picks out the salient points for distinguishing the taxon from its close relatives. These genera are distributed among the various families and subfamilies following the criteria outlined in the section above. In addition we also append to each genus a list

of species with their authors, original references and the geological horizon and brief locality of the holotype, together with a note of the major and most recent taxonomic revision if this has occurred. The species list is divided into 'species assigned', 'species questionably assigned' and 'species rejected' for each genus and is based partly on the inspection of original material in the British Museum (Natural History) and elsewhere and partly on inspection of the original published illustrations. Sadly, there is often a substantial difficulty in allocating species to genera, since this can only be done with any confidence when the brachial valve interior is adequately illustrated – it appears to us to be a waste of time and effort both in the past and future to try to describe formally and name any brachiopod without both interior and exterior illustration of both valves.

Superfamily PLECTAMBONITACEA Jones, 1928

- 1928 Plectambonitinae Jones: 394
 1929 Plectambonitidae Kozłowski: 108
 1952 Plectambonitacea Cooper & Williams: 332
 1953 Plectambonacea Williams: 6
 1965 Plectambonitacea Williams: H370
 1967 Plectambonitacea Havlíček: 26
 1970 Plectambonitacea Cocks: 154

DIAGNOSIS. Brachiopods with pseudopunctate shell: cardinal process simple or undercut, with a single process or trifold (although there are a few genera with no cardinal process), never bifid. Shell shape variable, but hinge line always straight.

DISCUSSION. The formal diagnosis of the Plectambonitacea is simplified. As far as is known, the acquisition of pseudopunctate only occurred once in the history of the Brachiopoda and thus the Plectambonitacea are a monophyletic group. However, they are also the stem group for the rest of the Strophomenida, and differ from other groups in that order only in the lack of bifid cardinal process. A few plectambonitaceans lack any cardinal process, but are clearly related in all other characters to other members of their assigned families, and the loss of the cardinal process in this superfamily can therefore be considered a secondary character.

RANGE. Lower Ordovician (U. Tremadoc) to Middle Devonian (Eifelian).

Family PLECTAMBONITIDAE Jones, 1928

- 1928 Plectambonitinae Jones: 394 *pars*
 1930 Plectambonitidae Öpik: 55 *pars*
 1930 Plectellinae Öpik: 55 *pars*
 1930 Plectambonitinae Öpik: 58 *pars*
 1933 Plectambonitidae Öpik: 9
 1938 Plectellinae Ulrich & Cooper: 185
 1953 Plectambonitidae Williams: 6 *pars*
 1956 Leptestiidae Cooper: 700 *pars*
 1956 Taphrodontidae Cooper: 742
 1965 Plectambonitidae Williams: H370
 1965 Leptestiidae Williams: H372 *pars*

DIAGNOSIS. Simple cardinal process, not undercut. No bema. Side-septa usually present.

REMARKS. The presence of a platform in all of the genera except *Isophragma* does not contribute to our diagnosis of

this family or its constituent subfamilies; however we do divide the family into two subfamilies, partly on the basis of the denticles to be found only in the Plectambonitinae and partly on the double septum to be found in the Taphrodontinae.

SUBFAMILIES ASSIGNED. Plectambonitinae Jones, 1928; Taphrodontinae Cooper, 1956.

RANGE. Upper Tremadoc to Lower Caradoc.

Subfamily PLECTAMBONITINAE Jones, 1928

- 1928 Plectambonitinae Jones: 394 *pars*
 1930 Plectellinae Öpik: 55 *pars*
 1930 Plectambonitinae Öpik: 58 *pars*
 1938 Plectellinae Ulrich & Cooper: 185
 1965 Plectambonitinae Williams: H370

DIAGNOSIS. Like Taphrodontinae, but with hinge-line denticles and without double median septum.

REMARKS. The presence of a platform in all the genera included in this subfamily does not, however, contribute to our diagnosis of the subfamily, neither do the presence of the pseudodeltidium and chilidium. Our family corresponds to the Plectambonitinae of the *Treatise* (Williams 1965) apart from the possible addition of *Akelina*. All three genera also have side septa within the pedicle valve.

GENERA ASSIGNED. *Ingria* Öpik, 1930 (including *Palinorthis* Ulrich & Cooper, 1936); *Plectambonites* Pander, 1830; *Plecttella* Lamansky, 1905; ?*Akelina* Severgina, 1967.

RANGE. U. Tremadoc (*Plecttella uncinata*) to L. Caradoc (*Plectambonites radiatus*).

INGRIA Öpik, 1930

Figs 6–11

- 1930 *Ingria* Öpik: 57
 1932 *Ingria* Öpik: 13
 1936 *Palinorthis* Ulrich & Cooper: 625
 1965 *Ingria* Williams: H370

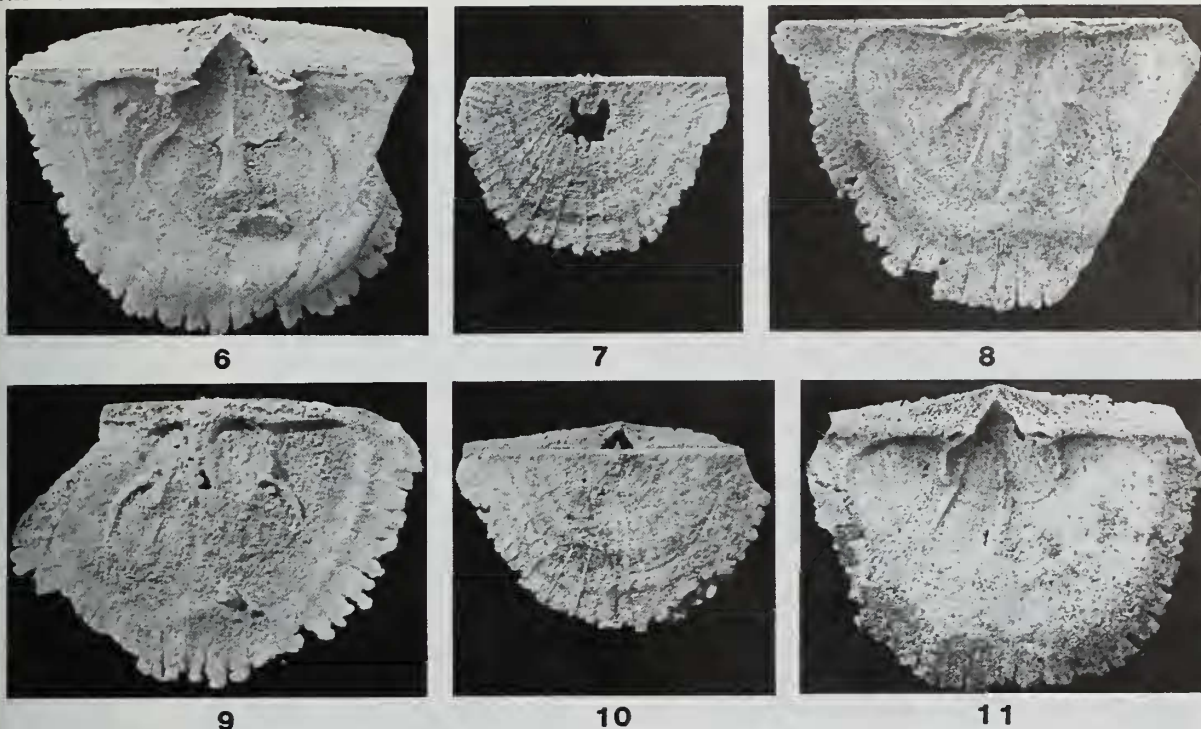
TYPE SPECIES. By original designation, *Orthisina nefedyevi* Eichwald, 1855. Type species of *Palinorthis* is *P. claudi* Ulrich & Cooper, 1936.

DIAGNOSIS. Flat to gently resupinate. Complex side septa similar to *Plectambonites*. Small pseudodeltidium, leaving delthyrium mainly open.

REMARKS. *Ingria* is a very variable genus, for example side septa are usually well developed, but the type species *Ingria nefedyevi* (Eichwald) almost lacks them (Öpik 1932: pl. 6, fig. 32). Because of this variability, we accept Cooper's (1938: 185) synonymy of *Ingria* with *Palinorthis* from Nevada.

SPECIES ASSIGNED.

- Ingria aka* Öpik, 1932: 32, pl. 9, figs 39, 40 from Arenig-Llanvirn beds, Obuchowa, near Wolchow, USSR.
Palinorthis claudi Ulrich & Cooper, 1936: 626 from the Upper Pogonip Fm. (Llanvirn) of Nevada, USA (revised Ulrich & Cooper 1938: 185; pl. 38, figs 4–8; pl. 57, figs 17–24).
Ingria expressa Öpik, 1932: 29; pl. 2, figs 10, 11 from the *Asaphus eichwaldi* beds (Llanvirn), Suhkrumägi, Tallinn, Estonia, USSR.



Figs 6–11 *Ingridia cloudi* (Ulrich & Cooper, 1936), topotypes, all silicified specimens from the *Orthidiella* Zone (L. Llanvirn), first ridge east of Frenchman's Flat, Nevada, USA. Fig. 6, pedicle valve interior BC 10312; Fig. 7, brachial valve exterior BC 10309; Fig. 8, brachial valve interior BC 10306; Fig. 9, brachial valve interior BC 10307; Fig. 10, exterior view of two conjoined valves BC 10313; Fig. 11, pedicle valve interior BC 10310. All $\times 3$.

Ingridia flabellum Öpik, 1932: 22; pl. 10, fig. 42 from Lower Llanvirn beds, Wassilkowo, USSR.

Ingridia holtedahli Öpik, 1939: 128; pl. 4, figs 3, 5–9 from Expansus Shale (L. Llanvirn), Krekling, Norway.

Ingridia malinovensis Andreeva, 1985: 40; pl. 4, figs 20–23 from Tarlikskaya Formation (Middle Ordovician), River Uyük, Tuva, USSR.

Orthisina nefedyevi Eichwald, 1855: pl. 36, fig. 13 from Expansus Beds, now Kunda Formation (L. Llanvirn), Isvos am Wolchow, Estonia, USSR (revised Öpik 1932: 17; pl. 6, fig. 32; pl. 7, fig. 34; pl. 10, figs 41, 43, 44).

Ingridia occidentalis Öpik, 1939: 129; pl. 3, fig. 12; pl. 5 figs 3–4 from Expansus Shale (L. Llanvirn), Hedenstad, Norway.

Ingridia pakriana Öpik, 1932: 23; pl. 1, figs 1–4; pl. 2 figs 7–9; pl. 6, fig. 33 from the Rogo Sandstones (L. Llanvirn), Paldiski, Estonia, USSR.

Ingridia sp. of Neuman 1977: 29; pl. 6, figs 19–23, 26–28, ?figs 24, 25, 29 from Arenig–Llanvirn of New World Island, Newfoundland, Canada.

Ingridia sp. A of Öpik 1932: 21; pl. 1, fig. 5 from Rogo Sandstone (L. Llanvirn), Halbinsel Paldiski, Estonia, USSR.

Ingridia sp. B of Öpik 1932: 29; pl. 1, fig. 6 from Rogo Sandstone (L. Llanvirn), Little Rogo Island, Estonia, USSR.

Ingridia sp. C of Öpik 1932: 31; pl. 2, fig. 13 from Megalaspid Limestone (U. Arenig), Little Rogo Island, Estonia, USSR.

SPECIES QUESTIONABLY ASSIGNED

Ingridia sp. Öpik, 1939: 129 (*Ingridia* ? sp. in pl. 4, fig. 4) from Expansus shale (L. Llanvirn), Krekling, Norway (only a single brachial valve external illustrated).

PLECTAMBONITES Pander, 1830

Fig. 12

1830	<i>Plectambonites</i> Pander: 90 <i>pars</i>
1892	<i>Plectambonites</i> Hall & Clarke: 295 <i>pars</i>
1933	<i>Plectambonites</i> Öpik: 11
1965	<i>Plectambonites</i> Williams: H370

TYPE SPECIES. *Plectambonites planissimus* Pander, 1830 [nom. correct. from *Plectambonites planissima* Pander] (subsequent designation Hall & Clarke 1892: 296).

DIAGNOSIS. Normal concavo-convex convexity. Similar to *Plectella* but more convex (sometimes geniculate) and with the side septa in the brachial valve more pronounced, more numerous and more complex. Chilidium and pseudodeltidium both pronounced.

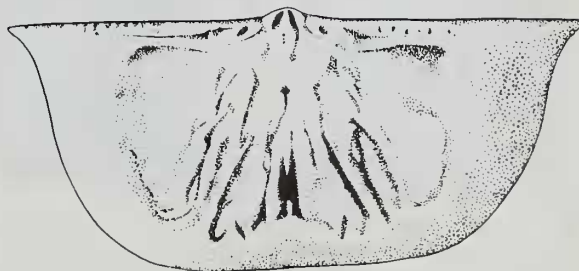


Fig. 12 *Plectambonites planissimus* Pander, 1830, from C_1 Beds (Llanvirn–Llandeilo), Baltic, USSR (after Williams 1965: fig. 237.2c), $\times 4$.

REMARKS. Pander (1930: 90), in erecting the genus *Plectambonites*, listed and briefly described twelve species, each of which, plus a further species *Plectambonites inversa*, were illustrated with two or three views on his pl. 19, all showing only the conjoined valve externals. In addition, on pl. 3, he depicted two views showing the interiors of a brachial and pedicle valve which he attributed to the genus *Plectambonites*, but without referring them to any particular species. All came from the St Petersburg (Leningrad) area, but without detailed locality data apart from a footnote (Pander 1830: 52) indicating that most of the shells came from the Iumalasaari, Peselowa and Podolowa areas, which all lie SSE of Leningrad in Upper Arenig, Llanvirn, and Llandeilo limestones. Hall & Clarke (1892) resuscitated the generic name and distinguished it from *Leptaena*, and attributed to it most of what we now know as the Plectambonitacea, although they also erected and separated off the *Leptella* group under that generic name, and furthermore erected *Christiania* (now a strophomenacean) to which they attributed one of Pander's species, *Plectambonites oblonga*.

SPECIES ASSIGNED

Plectambonites aranea Öpik, 1933: 14; pl. 1, figs 1–3 from C₁ Beds (Llanvirn–Llandeilo), Leningrad, USSR.

Plectambonites planissimus Pander, 1830: 90; pl. 19, fig. 1; neotype designated Öpik, 1933: 12; pl. 1, figs 4–6; pl. 3, fig. 2 from C₁ Beds (Llanvirn–Llandeilo), Pavlovsk, Leningrad, USSR.

Strophomena radiata Schmidt, 1858: 215; lectotype selected Öpik, 1930: 122; pl. 7, figs 82–83 from C₁–C₂ boundary beds (Llandeilo–Caradoc), Ärra, Estonia, USSR.

DOUBTFUL SPECIES (all from U. Arenig–Llandeilo, S of Leningrad, USSR):

Plectambonites convexa Pander, 1830: 91; pl. 91, fig. 5.

Plectambonites crassa Pander, 1830: 91; pl. 19, fig. 4.

Plectambonites inversa Pander, 1830: pl. 19, fig. 13.

Plectambonites lata Pander, 1830: 91; pl. 19, fig. 3.

Plectambonites ovata Pander, 1830: 92; pl. 19, fig. 9.

Plectambonites semiglobosa Pander, 1830: 91; pl. 19, fig. 8.

Plectambonites testudinata Pander, 1830: 91; pl. 19, fig. 6.

Plectambonites transversa Pander, 1830: 90; pl. 19, fig. 2.

Plectambonites triangularis Pander, 1830: 91; pl. 19, fig. 11.

SPECIES QUESTIONABLY ASSIGNED

Plectambonites? *jacuticus* Rozman, 1964: 146; pl. 14, figs 7–11 from U. Taryniuriakh Formation (M. Ordovician), Kalychan, Selenniakh Mountains, NE USSR (no interiors known).

SPECIES REJECTED

Plectambonites imbrex Pander, 1830: 91; pl. 19, fig. 12 (to Strophomenidae).

Plectambonites oblonga Pander, 1830: 92; pl. 19, fig. 10 (to *Christiania*).

Plectambonites uncinata Pander, 1830: 91; pl. 19, fig. 7 (to *Leptella*).

Plectambonites arca Shaler, 1865: 64; from Jupiter Formation (U. Llandovery), Anticosti Island, Quebec, Canada (transferred to *Brachyprion* by Twenhofel 1928: 189).

Plectambonites concentriliratus Grubbs, 1939: 556; pl. 62, figs 12, 15–17 from middle Silurian (probably Wenlock) nodules in dolomite, west Chicago, Illinois, USA (no interiors figured, but ornament, shape and outline all look like a pholidostrophid strophomenacean).

Plectambonites producta Hall & Clarke, 1894: 360; pl. 84, figs

23–25 from 'Niagara dolomites', Yellow Springs, Ohio, USA (shape and form appear to be like *Christiania*, but the locality information suggests a Silurian age: the species requires reinvestigation).

Plectambonites yenlacensis Mansuy, 1916: 49; pl. 7, fig. 3 from Kim-lu shales (?Ludlow), Kim-lu, Tonkin, Vietnam (no interiors known, but exteriors look similar to associated chonetaceans).

In addition, numerous subsequent authors, particularly before 1928, erected species originally ascribed to *Plectambonites*, but these are listed under their revised genera in this paper as well as being listed under *Plectambonites* in the index.

PLECTELLA Lamansky, 1905

1905 *Plectella* Lamansky: 156

1932 *Plectella* Öpik: 10

1933 *Plectella* Öpik: 16

1965 *Plectella* Williams: H372

TYPE SPECIES. *Plectambonites uncinata* Pander, 1830.

DIAGNOSIS. Normal convexity. Similar to *Plectambonites* but gentler convexity and with less pronounced side septa.

REMARKS. This is one of the earliest plectambonitaceans, but unfortunately the interior of the brachial valve is known only from the two rather poorly preserved specimens figured by Öpik (1933: pl. 4, figs 4, 5). The two specimens are from the same locality (not the type locality) but differ in strength of their side septa, the amount of secondary calcite around the cardinalia, and in the development of the platform. Further specimens, including brachial valve interiors, from the type locality and proper taxonomic revision are urgently needed.

SPECIES ASSIGNED

Plectambonites uncinata Pander 1830: 91 from B₁ beds with *Cyrtometopus primigenus* (U. Tremadoc), Maekula, 9 km west of Tallinn, Estonia, USSR (Öpik, 1933: 17; pl. 4, figs 2–5). Lamansky (1905: 159–60) also erected *Plectella gracilis*, *Plectella semiovalata*, *Plectella media*, *Plectella eminens*, *Plectella extensa* and *Plectella obtusa* all as new species, but all from the same locality of Popowka. Lamansky (1905: pl. 2) only figured exteriors of these species, and it is not known whether or not they all came from the same horizon, and their validity is doubtful.

?AKELINA Severgina, 1967

Figs 13–17

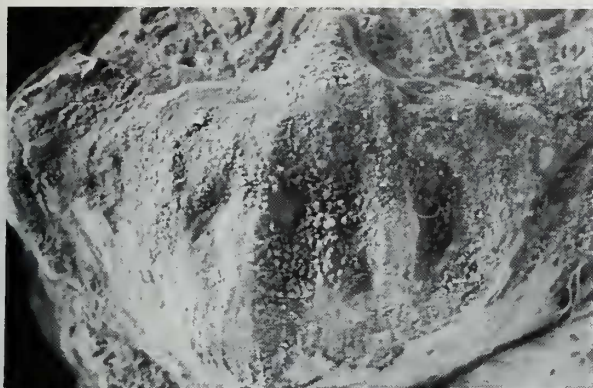
1967 *Akelina* Severgina: 133

1984b *Akelina* Severgina: 49

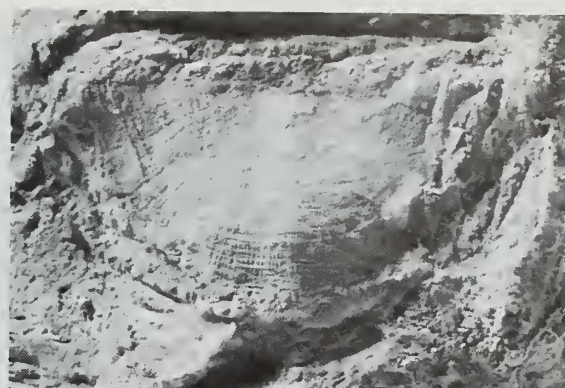
TYPE SPECIES. *Akelina akelina* Severgina, 1967.

DISCUSSION. There are various doubts still remaining about this genus, but because we consider that, on balance, it is probably a plectambonitacean and, if so, probably a member of the Plectambonitidae, we include it here, albeit with a query.

We are privileged in being able to examine and reillustrate the type specimens of the genus. They are preserved in a variety of lithologies, a partly exfoliated pedicle valve (Fig. 13) and a brachial valve exterior (Fig. 14) in limestone; two



3



14



a



15b



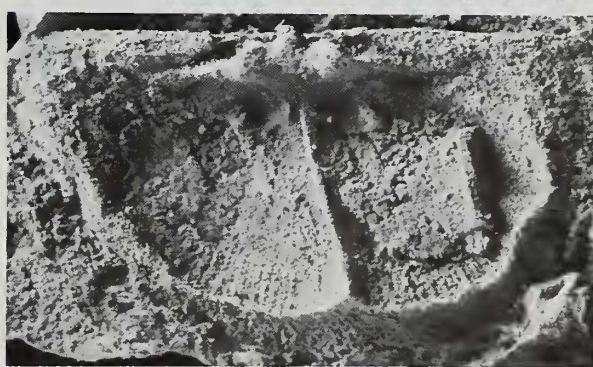
16a



16b



7a



17b

Figs 13–17 *Akelina akelina* Severgina, 1967, all from type locality in the Algan Formation (U. Tremadoc), River Akel, Kusnetz Alatai, Altai Mountains, USSR. Fig. 13, partly exfoliated interior of pedicle valve, the original of Severgina 1967: pl. 5, fig. 8, VSEGEI 424/1323, $\times 8$; Fig. 14, partly exfoliated exterior of brachial valve, the original of Severgina 1967: pl. 5, fig. 10, VSEGEI 425/1323, $\times 6$; Fig. 15, internal mould and latex cast of brachial valve, holotype, the original of Severgina 1967: pl. 5, fig. 9, VSEGEI 427/1323, $\times 6$; Fig. 16, latex cast and natural mould of pedicle valve exterior, the original of Severgina 1984: pl. 5, fig. 14, VSEGEI 1030/1323, $\times 6$; Fig. 17, natural mould and latex cast of brachial valve interior, VSEGEI 1027/1323, $\times 6$.

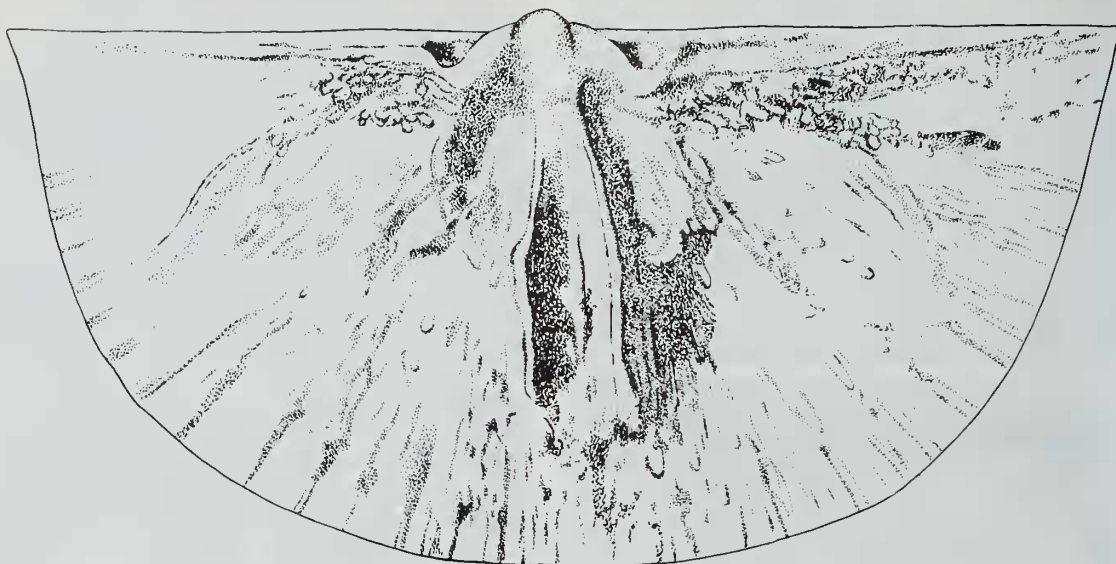


Fig. 18 *Isophragma ricevillense* Cooper, 1956, from base of Athens Formation (L. Caradoc), 4 km SSE of Riceville, Tennessee, USA, interior of brachial valve, based on BC 7211, $\times 12$.

brachial valves, including the holotype (Fig. 15), on a single block of grey decalcified sandstone; and one brachial valve (Fig. 17) in decalcified siltstone. This last specimen (Fig. 17) is the only one to have suffered tectonic distortion. Thus, because of the varied preservation, there is uncertainty as to whether a single stratigraphic unit and single species of brachiopod are really involved, but we have had to proceed on the assumption that all the specimens are truly conspecific. The partly exfoliated pedicle valve (Fig. 13) shows slight pimples, particularly near the umbo, which may be pseudopunctae, and it is on this basis that we provisionally accept *Akelina* as a plectambonitacean. The cardinal process and other details are not clear on the holotype, chiefly on account of the relatively coarse preservation, but the cardinal process appears to consist of a simple knob. On either side of the relatively strong myophragm of the holotype there is a pair of subparallel structures running anterolaterally; we interpret these as possible side septa, which is why the genus is assigned to the Plectambonitidae rather than to the Taffiidae, although on the other better preserved, but tectonically distorted, brachial valve (Fig. 17) these side septa are present only as faint traces.

The Tremadoc age of the material does not appear to be in doubt from the accompanying trilobites (Severgina 1984b), and, if *Akelina* is truly a plectambonitid, would be about the same age as the oldest member of the family, which is *Plectella* from the Baltic region.

In any case, a major reinvestigation of the genus from homogeneous large samples would be of great interest in clarifying the earliest history not only of the Plectambonitacea but the whole order Strophomenida.

SPECIES ASSIGNED

Akelina akelina Severgina, 1967: 133; pl. 5, figs 8–10 from Algan Horizon (U. Tremadoc), River Akel, Kuznetz Alatau, Altai-Sayan, USSR.

Subfamily TAPHRODONTINAE Cooper, 1956

1956	Isophragminae Cooper: 733
1956	Taphrodontidae Cooper: 740
1965	Isophragmatinae Williams: H375
1965	Taphrodontinae Williams: H376

DIAGNOSIS. Like Plectambonitinae, but with double median septum and without hinge line denticles.

REMARKS. It is difficult to find a precise term for the structure seen in the central part of the brachial valve in some taphrodontids. We term it a double septum, but the space between the two septa does not reach the valve floor, and thus the two side septa become united to form what might be termed a single median septum with a central hollow. However, this structure is unlike a normal median septum, and we analyse the double septum as analagous with side septa in other plectambonitaceans.

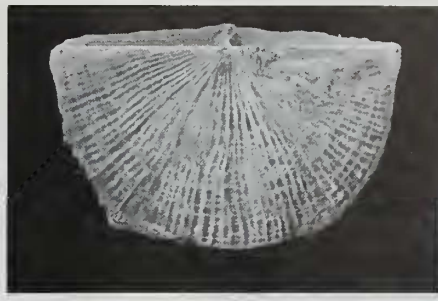
Even though Cooper (1956) erected separate familial or subfamilial rank for each of the two genera attributed to this subfamily, he did not directly compare the two, and we can find no subfamilial differences. The resupination which is often seen in *Isophragma* is regarded here as only of generic importance. We use the name Taphrodontinae rather than Isophragminae because, at the time of first erection of both, Cooper (1956) gave the taxon based on *Taphrodonta* familial rank rather than the subfamilial rank of the Isophragminae.

GENERA ASSIGNED. *Isophragma* Cooper, 1956; *Taphrodonta* (*Taphrodonta*) Cooper, 1956; *Taphrodonta* (*Nanambonites*) Liu, 1976.

RANGE. Llanvirn (*Nanambonites paucus*) to L. Caradoc (*Isophragma* spp.).



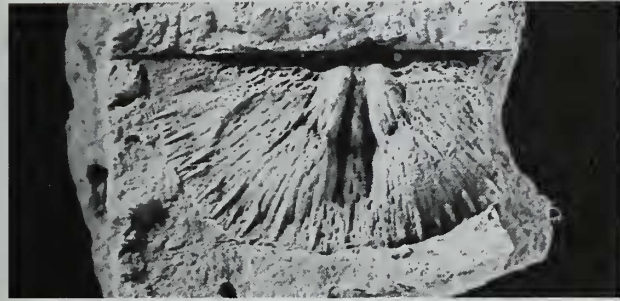
19a



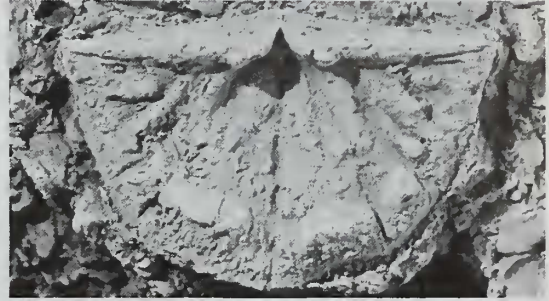
20a



20b



19b



21

Fig. 19 *Isophragma ricevillense* Cooper, 1956, topotype, from basal Athens Formation (L. Caradoc), 4 km SSE of Riceville, Tennessee, USA, latex cast and internal mould of brachial valve, BC 7211, $\times 4$.

Figs 20, 21 *Isophragma pseudoretroflexum* (Reed, 1917), topotypes from Balclatchie Conglomerate (L. Caradoc), Balclatchie, Girvan, Strathclyde, Scotland. Fig. 20, exterior of conjoined valves, the original of Reed 1917: pl. 13, figs 18, 18a, b, B73420, $\times 3$; Fig. 21, pedicle valve interior, the original of Reed 1917: pl. 13, fig. 20, B 73427, $\times 4$.

ISOPHRAGMA Cooper, 1956

Figs 18–21

1956 *Isophragma* Cooper: 733

1965 *Isophragma* Williams: H375

TYPE SPECIES. *Isophragma ricevillense* Cooper, 1956.

DIAGNOSIS. Flat to slightly resupinate. No accessory plates between cardinal process and interarea. Side septa variably developed, usually absent.

REMARKS. Sometimes (e.g. Fig. 19) the two central septa in the brachial valve can be traced separately throughout the length of the structure, but at other times the two septa are fused posteriorly to form a single broad structure.

SPECIES ASSIGNED

Isophragma biseptatum Cooper, 1956: 734; pl. 171, figs 20–32 from Benbolt Formation (L. Caradoc), Green Valley, Tennessee, USA.

Isophragma extensum Cooper, 1956: 735 from Arline Formation (L. Caradoc), Friendsville, Tennessee, USA, and subspecies *tricostatum* Williams, 1962: 162; pl. 15, figs 5, 7, 8–13 from Stinchar Limestone (Llandeilo), Girvan, Scotland.

Isophragma imperator Popov, 1980b: 147; pl. 2, figs 8–11 from Anderkensi Horizon (U. Llandeilo–L. Caradoc), Katnak Hill, Chu-Ili Mountains, Kazakhstan, USSR.

Isophragma orientale Andreeva, 1985: 40; pl. 4, figs 1–6 from Tarlikskaya Formation (M. Ordovician), River Uiuk, Tuva, USSR.

Isophragma princeps Popov, 1980a: 54; pl. 17, figs 1–7 from Erkebidaiski Horizon (M. Ordovician), Chelinograd, N. Kazakhstan, USSR.

Leptella? pseudoretroflexa Reed, 1917: 874; pl. 13, figs 18–26 from Balclatchie Conglomerate (L. Caradoc), Balclatchie,

Girvan, Scotland (revised Williams 1962: 162; pl. 15, figs 14–16, 20).

Isophragma ricevillense Cooper, 1956: 737; pl. 170, figs 1–15 from L. Athens Formation (L. Caradoc), Riceville, Tennessee, USA.

Isophragma subabbreviatum Cooper, 1956: 738; pl. 169, figs 1–9 from M. Arline Formation (L. Caradoc), Friendsville, Tennessee, USA.

SPECIES QUESTIONABLY ASSIGNED

Isophragma ponderosum Cooper, 1956: 737; pl. 210, figs 25–32 from Eureka Group (Llandeilo?), Martin Ranch, Roberts Mountains, Nevada, USA (no interiors figured).

Isophragma sulcatum Cooper, 1956: 739; pl. 170, fig. 16 from U. Llanvirn beds, Pratt Ferry, Alabama, USA (no interiors known).

Isophragma sp. 1 of Cooper 1956: 740; pl. 213, fig. 21 from Pratt Ferry Formation (Llanvirn), Pratt Ferry, Alabama, USA (may be *Syndielasma*).

TAPHRODONTA (TAPHRODONTA) Cooper, 1956

Figs 22, 23

1956 *Taphrodonta* Cooper: 740

1965 *Taphrodonta* Williams: H376

TYPE SPECIES. *Taphrodonta parallela* Cooper, 1956.

DIAGNOSIS. Like *Isophragma* but with no resupination, and shorter pedicle valve muscle field. Two small plates between cardinal process and interarea. No side septa apart from double median septum.

REMARKS. Although *Taphrodonta* has a generally simple cardinal process, in some specimens (e.g. Cooper 1956: pl.



22



23

Figs 22, 23 *Taphrodonta parallela* Cooper, 1956, topotypes from Upper Pogonip Group (U. Llanvirn), 1 mile above entrance to Ikes Canyon, Toquima Range, Nevada, USA. Fig. 22, pedicle valve interior, the original of Cooper 1956: pl. 165, figs 7–11, USNM 117562g, $\times 4$; Fig. 23, brachial valve interior, the original of Cooper 1956: pl. 165, figs 20–22, USNM 117562f, $\times 4$.

165, figs 19, 22) there are two very small plates in the chilidial opening between the cardinal process and the interarea; these are not fused to the cardinal process, and thus the cardinal process cannot be described as trifid.

SPECIES ASSIGNED

Taphrodonta parallela Cooper, 1956: 741; pl. 165, figs 1–22 from Antelope Valley Limestone, Upper Pogonip Group (U. Llanvirn), Ikes Canyon, Nevada, USA.

SPECIES QUESTIONABLY ASSIGNED

Taphrodonta bicornigera Nikitin, 1974: 58; pl. 5, figs 6–9 from Sarybidaik Formation (Llandeilo–Caradoc), right bank of Shiderty River, Narulgen, Kazakhstan, USSR (form of cardinal process uncertain from text and photographs).

TAPHRODONTA (NANAMBONITES) Liu, 1976

1976 *Nanambonites* Liu: 145

TYPE SPECIES. *Nanambonites paucus* Liu, 1976.

DIAGNOSIS. Like *Taphrodonta* (*Taphrodonta*) but with chilidium in brachial valve.

REMARKS. *Nanambonites* and *Taphrodonta* are the only two previously defined plectambonitacean genera with the two very small plates in the chilidial opening between the cardinal process and the interarea. The only difference we can find between them is the reported (but not illustrated) presence of a chilidium in *Nanambonites*, and this therefore merits their differentiation into separate subgenera. Liu (1976: 145) also mentioned the shape of the cardinal process and the shape of the double septum as generic differences, but the two taxa seem very similar to us in these respects.

SPECIES ASSIGNED

Nanambonites paucus Liu, 1976: 146; pl. 2, figs 17–19 from lower formation of Jiacun Group (Llanvirn), Mount Jolmo Lungma area, Tibet, China.

Family TAFFIIDAE Schuchert & Cooper, 1931

- 1931 Taffiinae Schubert & Cooper: 243
 1936 Taffiidae Ulrich & Cooper: 625
 1938 Taffiidae Ulrich & Cooper: 180
 1953 Taffiidae Williams: 6
 1965 Taffiidae Williams: H372 pars

DIAGNOSIS. Simple cardinal process. No bema. No side septa.

REMARKS. This family is divided into five subfamilies partly on the basis of shell shape, with the Ahtiellinae separated from the others by its resupination and geniculation, partly on the basis of the chilidium and muscle field, upon which the Spanodontinae differs from the rest, and partly on the platform, whose absence separates the Pelonomiinae from the others. The muscle field of the Spanodontinae is strikingly different in its dalmanelloid appearance as opposed to the more oblique arrangement of most plectambonitaceans, although *Taffia* itself, even though it is not well known, suggests a little similarity to *Spanodonta* in this feature. The Leptellinae is distinguished from the other subfamilies by the lack of a cardinal process; however, the morphology of its only genus, *Leptella*, is close to that of some taffiids, for example *Borua*.

SUBFAMILIES ASSIGNED. Taffiinae Schuchert & Cooper, 1931; Ahtiellinae Öpik, 1933; Leptellinae Williams, 1965; Pelonomiinae subfam. nov.; Spanodontinae subfam. nov.

RANGE. (? Tremadoc) Lower Arenig to Llandeilo.

Subfamily TAFFIINAE Schuchert & Cooper, 1931

- 1931 Taffiinae Schuchert & Cooper: 243
 1965 Taffiidae Williams: H372 pars
 1976 Aporthophylinae Liu: 143

DIAGNOSIS. Concavo-convex. With platform.

REMARKS. Liu (1976) established a new subfamily the Aporthophylinae based on the presence of a cardinal process and placed *Aporthophyla* and *Aporthophylina* with a cardinal process in it, as opposed to the Taffiinae, including *Taffia* alone, with no cardinal process. However, Neuman (1977) established that a cardinal process sometimes occurs within the type species of *Taffia*, and therefore we do not recognize Liu's subfamily.

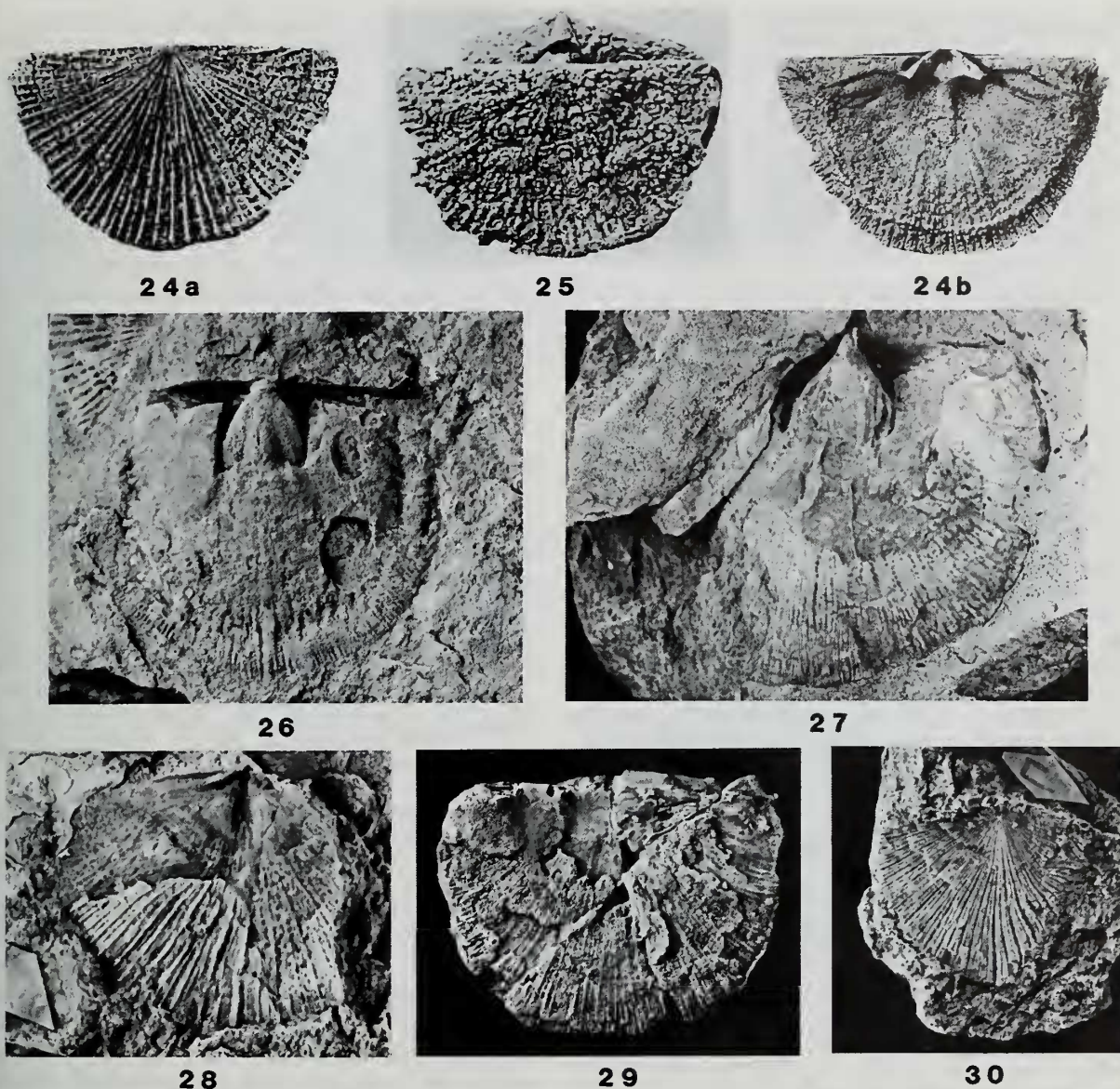
GENERA ASSIGNED. *Aporthophyla* Ulrich & Cooper, 1936, including *Archambona* Cooper, 1988; *Aporthophylina* Liu, 1976; *Taffia* Butts, 1926; *Tourmakeadia* Williams & Curry, 1985.

RANGE. L. Arenig (*Schedophyla striata*) to Llanvirn (several species, e.g. *Aporthophyla kasachstanica*).

APORTHOPHYLA Ulrich & Cooper, 1936

Figs 26–30

- 1936 *Aporthophyla* Ulrich & Cooper: 625
 1938 *Aporthophyla* Ulrich & Cooper: 182
 1965 *Aporthophyla* Williams: H372
 1970 *Aporthophyla* Ross: 63
 1974 *Aporthophyla* Neuman, in Neuman & Bruton: 85
 1987 *Aporthophyla* Ross & James: 83
 1988 *Archambona* Cooper: 186



Figs 24–25 *Taffia planoconvexa* Butts, 1926, from Odenville Formation (L. Arenig). Fig. 24, external and internal views of a brachial valve, the original of Ulrich & Cooper 1938: pl. 37, figs 15, 18 from railway east of Odenville Station, Alabama, USA, USNM 91586, $\times 3$; Fig. 25, conjoined valves, syntype, the original of Butts 1926: pl. 18, fig. 13 and Ulrich & Cooper 1936: pl. 37, fig. 16 from Newhope Church, 7 miles northeast of Pelham, Alabama, USA, USNM 71461b, $\times 3$.

Figs 26–30 *Aporthophyla typa* Ulrich & Cooper, 1936, from lower *Rhysostrophia* Zone, Upper Pogonip Group (Llanvirn), 1 mile above the entrance in Ikes Canyon, Toquima Range, Nevada, USA. Fig. 26, internal mould of pedicle valve, the original of Cooper 1956: pl. 163, fig. 24, USNM 117566, $\times 2$; Fig. 27, mostly exfoliated interior of pedicle valve, syntype, the original of Ulrich & Cooper 1938: pl. 37, fig. 2, USNM 92866a, $\times 2$; Fig. 28, mostly exfoliated interior of brachial valve, syntype, the original of Ulrich & Cooper 1938: pl. 37, figs 7, 8 USNM 92866e, $\times 3$; Fig. 29, conjoined valves USNM 92866c, $\times 2$; Fig. 30, external mould of brachial valve, syntype, the original of Ulrich & Cooper 1938: pl. 37, fig. 3, USNM 92866b, $\times 2$.

TYPE SPECIES. *Aporthophyla typa* Ulrich & Cooper, 1936 lectotype selected Neuman 1974: 85). Type of *Archambona* s. *A. floweri* Cooper, 1988.

DIAGNOSIS. Concavo-convex. Strong dental plates. Chilidium present, pseudodeltidium reduced or absent. Cardinal process always present.

REMARKS. *Aporthophyla* is very close to *Taffia*, particularly since a cardinal process is now known rarely from *Taffia* (Neuman 1977: 34), and also because Ross (1970: 63) dis-

covered a platform in specimens of *Aporthophyla*. In fact the two genera are only separated rigorously here on the size of the pseudodeltidium; however, in practice, specimens without a cardinal process are more likely to be *Taffia*. The types of *Aporthophyla* (Ulrich & Cooper 1938: pl. 37) include relatively small brachial valves (about 20 mm wide), none of which show a platform; however, a larger pedicle valve (Fig. 26, USNM 117566) shows slight traces of a platform, and many of the species listed below have platforms in much smaller specimens. All the features of *Archambona* agree

with those of *Aporthophyla* and we cannot separate these two genera.

SPECIES ASSIGNED

Strophomena aurora Billings, 1865: 218 from Table Head Formation (Llanvirn), Port Rich, Newfoundland, Canada (figured Cooper, 1956: pl. 164, figs 1–3 and Ross & James 1987: pl. 2, figs 11–14).

Archambona floweri Cooper, 1988: 186, figs 1.1–22 from Setul Formation (L. Ordovician), Pulau Langgun, Langkawi Islands, Malaysia.

Aporthophyla kasachstanica Rukavishnikova, 1956: 123; pl. 1, figs 6–9 from Kopalinski Horizon (Llanvirn), Kstau-sai, Chu-ili Mountains, Kazakhstan, USSR.

Aporthophyla perelegans Liu, 1976: 144; pl. 2, figs 1–9 from lower formation of Jiacun Group (U. Arenig–Llanvirn), Jiacun, Nielamu County, S. Xizang (Tibet), China (probably also includes '*Dactylogonia* sp.' of Liu 1976: 149; pl. 2, figs 10–11 from the same locality).

Aporthophyla stoermeri Neuman, in Neuman & Bruton 1974: 86, figs 4, 9, 10 from siltstone block of Llanvirn age, Trotland Farm, Hølonde, Norway.

Aporthophyla superstes Ross & James, 1987: 84; pl. 2, fig. 18; pl. 3, figs 1–4 from Table Point Formation (Llanvirn), Table Head, Newfoundland.

Aporthophyla tianjingshanensis Fu, 1982: 115; pl. 34, figs 2–6 from the Tianjingshan Formation (U. Arenig), Tianjingshan, Zhongwei, Ningxia Province, N. China.

Aporthophyla tyra Ulrich & Cooper, 1936: 625 from the Upper Pogonip Group (Llanvirn), Ikes Canyon, Nevada, USA (revised Ulrich & Cooper, 1938: 183; pl. 37, figs 1–3, 5, 7, 8, 10, 11).

SPECIES QUESTIONABLY ASSIGNED

Aporthophyla ordensis Klenina, 1984: 64; pl. 5, figs 16, 18, 19; pl. 6, figs 7, 10, 14 from Abaevskaya Formation (Llanvirn–Llandeilo), SE Ordatas Hill, Pre-Chinghiz Mountains, Kazakhstan, USSR (no interiors illustrated).

Aporthophyla sp. of Liu *et al.* 1983: 273; pl. 92, figs 18–20 from Majiagou Formation (Llanvirn), Xiaoxian County, Anhui Province, China (no interiors known).

APORTHOPHYLINA Liu, 1976

1976 *Aporthophylina* Liu: 144

TYPE SPECIES. *Aporthophylina intermedia* Liu, 1976.

DIAGNOSIS. Like *Aporthophyla* but lacking dental plates in pedicle valve.

REMARKS. According to Liu (1976: 144), *Aporthophylina* differs from *Aporthophyla* in its socket ridges, in a cardinal process which becomes stronger posteriorly, in a long strong median ridge in the brachial valve, and in the lack of dental plates in the pedicle valve. We do not consider the first three characters to be of generic importance, but continue to separate the two genera on the absence of dental plates.

SPECIES ASSIGNED

Aporthophylina intermedia Liu, 1976: 145; pl. 2, figs 12–15 from lower formation of Jiacun Group (U. Arenig–Llanvirn), Chaya, Dingri County, Xizang (Tibet), China.

TAFFIA Butts, 1926

Figs 24, 25

1926 *Taffia* Ulrich MS in Butts: 99
1938 *Taffia* Ulrich & Cooper: 180
1956 *Taffia* Cooper: 697
1965 *Taffia* Williams: H372
1977 *Taffia* Neuman: 34

TYPE SPECIES. *Taffia planoconvexa* Butts, 1926.

DIAGNOSIS. Usually without simple cardinal process (but may be rarely present). Large pseudodeltidium, small chilidium also present.

REMARKS. Earlier authors (Ulrich & Cooper 1936, 1938, Williams 1965) stressed the absence of a cardinal process as part of their diagnosis of *Taffia*, but Neuman (1977: 34) described great variation in this respect; in a population of 12 specimens from the Odenville Limestone of Alabama, 3 have a low but definite simple cardinal process whilst in 9 the floor of the notothyrial platform is smooth. Until the occasional presence of a cardinal process is demonstrated in some other population of *Taffia* we think that it is better to keep *Taffia* and *Aporthophyla* as distinct genera.

SPECIES ASSIGNED

Taffia anomala Benedetto & Herrera 1986: 117; pl. 3, figs 1–13 from U. San Juan Formation (M. Arenig–L. Llanvirn), Quebradas Honda, San Juan Province, Argentina.

Taffia planoconvexa Butts, 1926: 100; pl. 18, figs 13–17 from the Odenville Formation (L. Arenig), Odenville, Alabama, USA (revised Ulrich & Cooper, 1938: 181; pl. 37, figs 12–18).

Taffia westgatei Ulrich & Cooper, 1936: 625 (figd Ulrich & Cooper 1938: pl. 37, figs 4, 6, 9) from Yellow Hill Formation (Arenig–Llanvirn), Ely Springs Range, Nevada, USA.

Taffia ? sp. of Neuman 1977: 34; pl. 7, figs 16–21; pl. 8, fig. 2 from Llanvirn rocks, Virgin Arm, Newfoundland, Canada.

TOURMAKEADIA Williams & Curry, 1985

1985 *Tourmakeadia* Williams & Curry: 252

TYPE SPECIES. *Tourmakeadia fimbriata* Williams & Curry, 1985.

DIAGNOSIS. With elevated and bilobed platform in pedicle valve.

REMARKS. Even though the cardinal process is clearly that of a taffiid, nevertheless the rest of the morphology (apart from the interesting pedicle valve platform) is very close to *Leptellina* and its relatives in the Leptellinidae, and some form related to *Tourmakeadia* was probably the ancestor of *Leptellina*.

SPECIES ASSIGNED

Tourmakeadia fimbriata Williams & Curry, 1985: 253, figs 176–182 from Tourmakeady Limestone (U. Arenig), Tourmakeady, Co. Mayo, Ireland.

Subfamily **AHTIELLINA**E Öpik, 1933

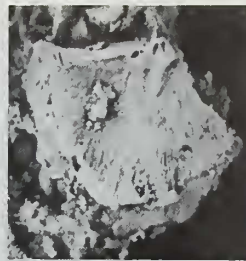
1933 Ahtiellinae Öpik: 19
1953 Ahtiellinae Williams: 6
1965 Ahtiellinae Williams: H372



3 1



3 2



3 3



3 4

Figs 31–34 *Borua modesta* Williams & Curry, 1985, from Tourmakeady Limestone (U. Arenig), stream 2 km SW of Srah Bridge, Co. Mayo, Ireland. Fig. 31, internal view of pedicle valve, paratype, the original of Williams & Curry 1985: fig. 171, BB 95532, $\times 3$; Fig. 32, interior of brachial valve, holotype, the original of Williams & Curry 1985: fig. 171, BB 95531, $\times 3$; Fig. 33, interior of brachial valve, the original of Williams & Curry 1985: fig. 173, BB 95533, $\times 3$; Fig. 34, exterior of brachial valve, the original of Williams & Curry 1985: fig. 175, BB 95537, $\times 4$.

DIAGNOSIS. Resupinate. With platform (or diaphragm).

REMARKS. Both Öpik (1933) and Williams (1965) included the Ahtiellinae as a subfamily within the Plectambonitidae, but we include the subfamily within the Taffiidae owing to the absence of side septa.

GENERA ASSIGNED. *Ahtiella* Öpik, 1932; *Borua* Williams & Curry, 1985; *Guttasella* Neuman, 1977; *Inversella* (Inversella) Öpik, 1933; *Inversella* (Reinversella) Bates, 1968; *Rutrumella* Harper, 1981; *Sanjuanella* Benedetto & Herrera, 1987; *Schedophyla* Neuman, 1971.

RANGE. U. Arenig (*Ahtiella quadrata*) to Llanvirn–Llandeilo (*Ahtiella lirata*).

AHTIELLA Öpik, 1932

1932 *Ahtiella* Öpik: 37
1933 *Ahtiella* Öpik: 19
1965 *Ahtiella* Williams: H372

TYPE SPECIES. *Ahtiella lirata* Öpik, 1932.

DIAGNOSIS. With brachial valve median septum and with impersistent rugae and simple geniculation. Relatively small socket plates.

REMARKS. *Ahtiella* may be distinguished from *Inversella* by the presence of a brachial valve median septum and impersistent rugae. *Guttasella* differs in its double geniculation and in lacking both a brachial valve median septum and also rugae. Hessland (1949) lists the various ornamental differences which he considered important in distinguishing species; however, a further revision might show that many of the names listed below should properly be synonymized with each other.

SPECIES ASSIGNED

Ahtiella arenaria Öpik, 1933: 19; pl. 4, figs 7, 8 from Rogö Lime-Sandstone (Llanvirn), Little Rogö Island, Estonia, USSR.
Ahtiella argentina Benedetto & Herrera, 1986: 114; pl. 1, figs 4–21 from U. San Juan Formation (L. Llanvirn), Quebradas Los Gatos y Honda, San Juan province, Argentina.
Ahtiella baltica Öpik, 1932: 42; pl. 2, fig. 12; pl. 5, fig. 1, from Rogö Sandstone, B_{iii} (Llanvirn), Paldiski, Estonia, USSR.
Ahtiella concava Bates, 1968: 167; pl. 7, figs 12–22 from Bod Deiniol Formation (Llanvirn), Bod Deiniol, Anglesey, Wales.

Ahtiella jaanussoni Hessland, 1949: 523; pl. 1, fig. 2 from *raniceps* Zone Beds (Llanvirn), Hälluden, Öland, Sweden.
Ahtiella lirata Öpik, 1932: 39; pl. 3, figs 14–21; pl. 5, fig. 31; pl. 8, figs 36–37 from C₁ Beds (Llanvirn–Llandeilo), Tsitri, Estonia, USSR.

Ahtiella paucirugosa Neuman, 1977: 30; pl. 3, figs 24–37; pl. 8, fig. 1 from Llanvirn rocks, Virgin Arm, Newfoundland, Canada.

Ahtiella quadrata Bates, 1968: 166; pl. 8, figs 1–9 from Torllwyn Formation (Arenig), Ogof Gynfor, Anglesey, Wales.

SPECIES QUESTIONABLY ASSIGNED

Ahtiella dalecarlia Hessland, 1949: 520; pl. 1, figs 3–5 from 3 m above *limbata* Limestone (Llanvirn), Leskusänget, Orsa, Dalarna, Sweden (no interiors figured).

Leptaena gemella Eichwald, 1860: 861; pl. 36, fig. 6 from Lower Ordovician beds, Pulkowa, nr Leningrad, USSR (no interiors figured).

Strophomena jentzschii Gagel, 1980: 44; pl. 5 fig. 26 from glacial erratics in N. Germany of unknown age (assigned to *Ahtiella* by Hessland (1949: 518; pl. 1, figs 1, 2) and Sokolskaya (1960: pl. 27, figs 9, 10) but no interiors figured).

Ahtiella oelandica Hessland, 1949: 521; pl. 2, figs 1, 3, 4 from *raniceps* Zone Beds (Llanvirn), Stenasa, Öland, Sweden (no interiors figured).

Ahtiella plana Hessland, 1949: 524; pl. 1, figs 6, 7 from *raniceps* Zone beds (Llanvirn), Hälluden, Öland, Sweden (no interiors figured).

SPECIES REJECTED

Ahtiella ? portlocki Reed, 1952: 48; pl. 2, fig. 5 from Killey Bridge Formation (L. Ashgill), Pomeroy, County Tyrone, Northern Ireland (revised Mitchell 1977: 114; pl. 26, figs 1–13 and assigned to *Brachyprion*; reassigned to *Pholidostrophia* (*Eopholidostrophia*) by Cocks 1978: 129).

BORUA Williams & Curry, 1985 Figs 31–34

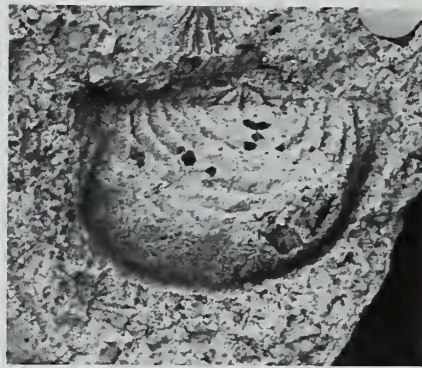
1985 *Borua* Williams & Curry: 250

TYPE SPECIES. *Borua modesta* Williams & Curry, 1985.

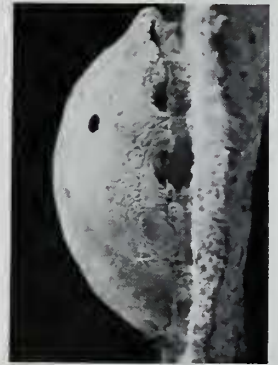
DIAGNOSIS. Smooth apart from faint peripheral parvicostellae and occasional impersistent rugae in some specimens. Short



35a



35b



36



37a



38



37b



39

Fig. 35 *Inversella* (*Reinversella*) *monensis* Bates, 1968, exterior and counterpart interior moulds of brachial valve, holotype, the original of Bates 1968: pl. 8, figs 10–12, BB 30574, from Treiorwerth Formation (Arenig), 300 yards SE of Ffynnon-y-mab, Trefor, Anglesey, Wales, $\times 2$. **Figs 36–39** *Spanodonta hoskingiae* Prendergast, 1935, topotypes from Gap Creek Formation (Middle Ordovician), south side of Gap Spring, Price's Creek, Emmanuel Range, Western Australia. Fig. 36, lateral view of pedicle valve, BC 10604, $\times 3.5$; Fig. 37, a brachial valve interior viewed obliquely from the posterior and straight down, BC 10605, $\times 3$ and $\times 3.5$; Fig. 38, brachial valve interior, BC 7238, $\times 4$; Fig. 39, conjoined valves partly exfoliated to show the pedicle valve muscle field and part of the brachial valve platform, BC 7242, $\times 4$.

myophragm in brachial valve, but no brachial valve median septum.

REMARKS. The smooth shell surface (apart from peripheral parvicostellae and occasional rugae) is not known elsewhere in the family. It may be the result of silicification processes in the only known specimens, but if original then the cause is unknown, as is the function of parvicostellae generally.

SPECIES ASSIGNED

Borua modesta Williams & Curry, 1985: 250, figs 169–175 from Tourmakeady Limestone (U. Arenig), Tourmakeady, Co. Mayo, Ireland.

GUTTASELLA Neuman, 1977

1977 *Guttasella* Neuman: 31

TYPE SPECIES. *Guttasella gutta* Neuman, 1977.

DIAGNOSIS. No rugae. No brachial valve median septum. Doubly geniculate like *Inversella* (*Reinversella*).

REMARKS. *Guttasella* is similar to *Reinversella* and differs externally in the lack of rugae. The cardinalia and shell shape indicate the placing of this genus within the Ahtiellinae. However, one of Neuman's illustrations (1977: pl. 5, fig. 4) indicates the slight trace of a bema, a feature which is

generally absent in the Taffiidae; nevertheless we prefer to assign the genus here.

SPECIES ASSIGNED

Tuttasella gutta Neuman, 1977: 31; pl. 5, figs 1–5 from Llanvirn age rocks, Virgin Arm, Newfoundland, Canada.

INVERSELLA (INVERSELLA) Öpik, 1933

933 *Inversella* Öpik: 21

965 *Inversella* Williams: H372

TYPE SPECIES. *Inversella borealis* Öpik, 1933.

DIAGNOSIS. No median septum in brachial valve. Persistent rugae over valve and strongly geniculate in a ventral direction.

SPECIES ASSIGNED

Inversella angulata Öpik, 1933: 23; pl. 3, fig. 3 from B_{III} (L. Llanvirn), Toila, Estonia, USSR.

Inversella borealis Öpik, 1933: 23 (figured as *Palaeostrophomena concava* by Öpik 1932: pl. 4, fig. 24) from the Echinospaeriten Limestone C_{1a} (U. Llanvirn), Eesti, Estonia, USSR.

Inversella sp. of Neuman 1977: 34; pl. 6, figs 1–4 from Llanvirn age rocks, Virgin Arm, New World Island, Canada.

SPECIES QUESTIONABLY ASSIGNED

Inversella perundosa Öpik, 1939: 128; pl. 5, fig. 6 from the Expansus Shale (L. Llanvirn) of Rokstadasen, Hedenstad, Norway (only pedicle valve exterior illustrated – the species could be a leptaenid).

INVERSELLA (REINVERSELLA) Bates, 1968

Fig. 35

968 *Reinversella* Bates: 169

TYPE SPECIES. *Reinversella monensis* Bates, 1968.

DIAGNOSIS. Like *Inversella* (*Inversella*) with second deflection of the anterior and lateral borders. With continuous rugae.

REMARKS. The close similarity between *Inversella* and *Reinversella* leads us to place the latter as a subgenus within the former.

SPECIES ASSIGNED

Reinversella arancibiai Herrera & Benedetto, 1987: 78, figs 2a–c from upper part of San Juan Formation (Llanvirn), Quebrada Los Gatos, west flank of Cerro Viejo, San Juan, Argentina.

Reinversella monensis Bates, 1968: 169; pl. 8, figs 10–17 from Treiorwerth Formation (Arenig), Ffynnon-y-mab, Anglesey, Wales.

RUTRUMELLA Harper, 1981

981 *Rutrumella* Harper in Bruton & Harper 1981: 163

TYPE SPECIES. *Rutrumella implexa* Harper, 1981.

DIAGNOSIS. Resupinate. Differs from *Schedophyla* in having discontinuous rugae, not geniculate. Relatively large socket plates.

REMARKS. This resupinate genus has a distinctive ornament of discontinuous rugae. No pedicle valves and only three brachial

valves are known, all as internal moulds with no definite proof of a pseudopunctate shell structure. The only cardinal process illustrated is similar to other taffiids, although it appears incomplete posteriorly. The muscle scars shown (Bruton & Harper 1981: pl. 2, figs 12, 13) are very indistinct, but appear similar to some contemporary Orthacea and Clitambonitacea. The genus is described as lacking radial ornamentation, but the preservation appears too coarse to exclude its possibility. Thus the plectambonitacean affinities of this genus are uncertain, although the genus is placed here in the Ahtiellinae.

SPECIES ASSIGNED

Rutrumella implexa Harper, in Bruton & Harper 1981: 164; pl. 2, figs 9, 12, 15 from Otta Conglomerate (Llanvirn), Otta, Norway.

SANJUANELLA Benedetto & Herrera, 1987

1987 *Sanjuanella* Benedetto & Herrera: 103

TYPE SPECIES. *Sanjuanella plicata* Benedetto & Herrera, 1987.

DIAGNOSIS. Myophragm but no brachial valve median septum. Relatively small pedicle valve muscle field and small socket plates in brachial valve. Like *Borua* but with marked parvicostellate ornament.

REMARKS. Although the material is somewhat scrappy, the two illustrated brachial valve interiors show the simple cardinal process and lack of side septa clearly, making the new genus definitely attributable to the Taffiidae, rather than to the Plectambonitidae where it was placed by its authors.

SPECIES ASSIGNED

Sanjuanella plicata Benedetto & Herrera, 1987: 104; pl. 1, figs 1–14 from upper part of San Juan Formation (Llanvirn), Quebrada Honda, west flank of Cerro Viejo, San Juan Province, Argentina.

SCHEDOPHYLA Neuman, 1971

1971 *Schedophyla* Neuman: 120

1984 *Schedophyla* Xu & Liu: 200

TYPE SPECIES. *Schedophyla potteri* Neuman, 1971.

DIAGNOSIS. Very similar to *Aporthophyla* but resupinate. Differs from *Rutrumella* in having radial ornamentation and no rugae.

REMARKS. The shell structure has not been determined since the New Brunswick material consists entirely of moulds; it is possible that the genus is an orthid. Neuman (1971:120) considered the genus to be 'most similar to *Ahtiella*' but this is true only of the valve form; the remaining characters appear identical to *Aporthophyla*, in particular the ventral muscle field and the cardinalia.

SPECIES ASSIGNED

Schedophyla minor Xu & Liu, 1984: 202; pl. 14, figs 15, 16, 21 from Meitan Formation (Arenig), Nanzhang, W. Hubei, China.

Schedophyla potteri Neuman, 1971: 122; pl. 2, figs 1–11 from Tuffaceous sandstone (Llanvirn?), middle Haydon Brook, York County, New Brunswick, Canada.

'*Hesperonomia*' *striata* Xu, Rong & Liu, 1974: 144; pl. 64, figs 29–31 from Lower Meitan Formation (L. Arenig), Sinan, NE Guizhou, China.

Schedophyla subquadrata Xu & Liu, 1984: 201 *pars*; pl. 14, figs 30, 31, *non* fig. 20; pl. 15, figs 6–8, 20 from Lower Meitan Formation (L. Arenig), Yanhe, NE Guizhou, China.

SPECIES QUESTIONABLY ASSIGNED

Schedophyla interrupta Xu, in Liu *et al.* 1983: 276; pl. 92, figs 10–12 from U. Dawan Formation (U. Arenig), Nanjing, Jiangsu Province, China (no interiors known).

Schedophyla sp. of Xu & Liu 1984: 202; pl. 15, fig. 9 from Lower Meitan Formation (Arenig), Yanhe, NE Guizhou, China (no brachial valve interior known).

Subfamily PELONOMIINAE *nov.*

DIAGNOSIS. Not resupinate, although fairly flat. No platform.

REMARKS. *Pelonomia* is difficult to place, except that it is undoubtedly a plectambonitacean. It is close to the Taffiinae, but has no platform and we therefore erect a new subfamily for the genus.

GENUS ASSIGNED. *Pelonomia* Cooper, 1956.

RANGE. Llanvirn.

PELONOMIA Cooper, 1956

1956 *Pelonomia* Cooper: 699

1965 *Pelonomia* Williams: H372

TYPE SPECIES. *Orthis delicatula* Billings, 1865.

DIAGNOSIS. Slight fold in pedicle valve with corresponding sulcus in brachial valve. Larger pseudopunctae seen on dorsal sulcus.

REMARKS. The only species is small, but it is distinctive and difficult to place systematically. Pseudopunctae are clearly visible and there is a simple single cardinal process, and so it is undoubtedly a plectambonitacean. However, the specimens illustrated so well by Cooper (1956: pl. 223) are not the original type specimens of Billings, and until the latter are revised, there must remain some doubt as to the identity of the species and genus.

SPECIES ASSIGNED

Orthis delicatula Billings, 1865: 217 (revised by Cooper 1956: 699; pl. 223, figs 8–10) from the Table Head Formation (Llanvirn) near Table Head, Newfoundland, Canada.

Subfamily SPANODONTINAE *nov.*

DIAGNOSIS. Normal convexity. Distinctive 'dalmanelloid' brachial valve muscle field. With chilidium. With platform.

DISCUSSION. The distinctive 'dalmanelloid' brachial valve muscle field, with the transverse ridge separating the two pairs of muscle scars, is unique among the Plectambonitacea (except possibly for the unplaced genus *Rutrumella*). This feature alone certainly merits subfamilial recognition to separate it from the rest of the Taffiidae. *Spanodonta* is only

known from silicified specimens, and thus its strophomenoid assignment is only based on a general similarity to the taffids and other plectambonitaceans. It also bears some resemblance to *Eostrophomena* Walcott, 1905, from the latest Tremadoc of Sweden, which has been assigned to the Orthidiellidae by Williams (1965: H309–310), and whose shell composition is also undocumented.

GENUS ASSIGNED. *Spanodonta* Prendergast, 1935.

RANGE. Llanvirn–Llandeilo.

SPANODONTA Prendergast, 1935
Figs 36–40

1935 *Spanodonta* Prendergast: 12

1965 *Spanodonta* Williams: H375

1987 *Spanodonta* Laurie: 44

TYPE SPECIES. *Spanodonta hoskingiae* Prendergast, 1935.

DIAGNOSIS. As for subfamily. The cardinal process is not trilobed (*contra* Williams 1965: H375) and consists of a simple ridge.

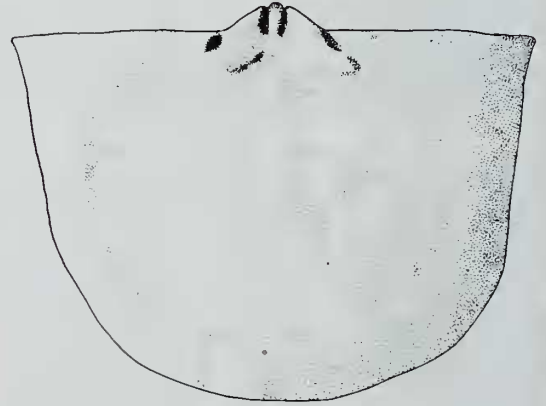


Fig. 40 *Spanodonta hoskingiae* Prendergast, 1935, from Gap Creek Formation (Middle Ordovician), south side of Gap Spring, Price's Creek, Emmanuel Range, Western Australia, interior of brachial valve, based on BC 7238 and BC 10605, $\times 5$.

REMARKS. *Spanodonta* was originally described as a productacean from the Carboniferous of Western Australia, but was reassigned to the Plectambonitacea when the Ordovician age of the beds became known. A good new collection of topotype material made by the British Museum (Natural History) expedition to Western Australia in 1966 enables us to illustrate the genus properly (Figs 36–40) as has Laurie (1987). We agree with Laurie's assignment of the genus to the Taffiidae, but do not think that it was so closely related to *Aporhophyla* as he thought (1987: 44, figs 2, 3).

SPECIES ASSIGNED

Spanodonta hoskingiae Prendergast, 1935: 13; pl. 3, figs 1–3 from Gap Creek Formation (Lower to Middle Ordovician), Price's Creek, Kimberley, Western Australia (revised Laurie 1987: 44, figs 2–3).

SPECIES REJECTED

Spanodonta tingriensis Liu, 1976: 146; pl. 2, figs 24–31 from a pebble of Ordovician age, Bensai, Dingri County, Xizang



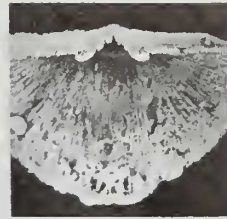
4 1



4 2



4 3



4 4

Figs 41–44 *Leptella musculosa* Williams & Curry, 1985, topotypes from Tourmakeady Limestone (U. Arenig), stream 2 km SW of Srah Bridge, Co. Mayo, Ireland. Fig. 41, conjoined valves, holotype, the original of Williams & Curry 1985: fig. 183, BB 95546, $\times 5$; Fig. 42, brachial valve interior, the original of Williams & Curry 1985: fig. 188, BB 95547, $\times 5$; Fig. 43, brachial valve interior, the original of Williams & Curry 1985: fig. 184, BB 95549, $\times 5$; Fig. 44, central part of pedicle valve interior, the original of Williams & Curry 1985: fig. 186, BB 95548, $\times 5$.

(Tibet), China (because of the trifid cardinal process this species should be placed within the Leptellinidae, but the true genus is uncertain).

Subfamily LEPTELLINAE Williams, 1965

- 1936 Leptellininae Ulrich & Cooper: 626 *pars*
 1938 Leptellininae Ulrich & Cooper: 187 *pars*
 1965 Leptellininae Williams: H376

DIAGNOSIS. Leptellinidae without cardinal process.

REMARKS. Both nominal genera in the subfamily possess a platform and they are united here as subgenera within a single genus. Obviously, since they lack a cardinal process, their assignment to the Taffiidae must then remain a little doubtful. However, *Leptella* and *Petroria* are otherwise very similar to *Taffia* and its relatives, which causes us to place the Leptellinae within the Taffiidae. This differs from Williams (1965) in the *Treatise on Paleontology*, who placed the Leptellinae within the Leptellinidae; however *Leptella* and *Petroria* are so much older than the rest of the Leptellinidae that they would seem very unlikely to be either the direct ancestors or descendants of forms with trifid cardinal processes.

GENERA ASSIGNED. *Leptella* (*Leptella*) Hall & Clarke, 1892; *Leptella* (*Petroria*) Wilson, 1926.

RANGE. Possibly Tremadoc (*Leptella exigua*) but definitely L. Arenig (*Leptella hubeiensis*) to Arenig–Llanvirn boundary beds (*Leptella sordida*).

LEPTELLA (LEPTELLA) Hall & Clarke, 1892

Figs 41–44

- 1892 *Leptella* Hall & Clarke: 293
 1938 *Leptella* Ulrich & Cooper: 187
 1965 *Leptella* Williams: H377

TYPE SPECIES. *Leptaena sordida* Billings, 1862.

DIAGNOSIS. Median septum not anterior of the platform in the brachial valve.

SPECIES ASSIGNED

- Leptella grandis* Xu, Rong & Liu, 1974: 149; pl. 65, figs 14–17 from Lower Meitan Formation (L. Arenig), Sinan, Sinan County, NE Guizhou, China.
Leptella hubeiensis Zeng, 1977: 57; pl. 20, figs 1–3 from L.

Dawan Formation (M. Arenig), Fenxian, Yichang County, W. Hubei Province, China.

Leptella musculosa Williams & Curry 1985: 254, figs 183–189 from Tourmakeady Limestone (U. Arenig), Tourmakeady, Co. Mayo, Ireland.

Leptaena sordida Billings, 1862: 74, fig 66 from Limestone No 2 (Arenig–Llanvirn Boundary), Point Lévis, Quebec, Canada (revised Ulrich & Cooper 1938: 189; pl. 39, figs 17–21, 23–33).

SPECIES QUESTIONABLY ASSIGNED

Leptella? *exigua* Clark, 1924: 84; pl. 8, fig. 13 from *Shumardia* Zone of Beekmantown Series (Tremadoc), Lévis, Quebec, Canada (no interiors figured).

Leptella nevadensis Ulrich & Cooper, 1938: 189; pl. 39, figs 16, 22 from Billingsura Zone of U. Pogonip (Llanvirn), Antelope Range, Nevada, USA (no interiors known).

LEPTELLA (PETRORIA) Wilson, 1926

- 1926 *Petroria* Wilson, 1926
 1956 *Petroria* Cooper, 746
 1965 *Petroria* Williams: H378
 1987 *Petroria* Ross & James: 84

TYPE SPECIES. *Petroria rugosa* Wilson, 1926.

DIAGNOSIS. Like *Leptella* (*Leptella*) but with median septum continuing anteriorly of the platform in brachial valve.

REMARKS. The type species was originally described as from the Beaverfoot Formation which is of Ashgill age, but Cooper (1956: 746) suggests that the specimens are more probably of Arenig age. This was confirmed by Norford (1969: 37), who reassigned the type locality to the Lower Ordovician Skoki Formation. We are most grateful to Dr B. S. Norford, who has provided us with copies of his unpublished notes and illustrations of *P. rugosa*. These confirm that the genus is closely related to *Leptella*, but differs in the length of the median septum in the brachial valve.

SPECIES ASSIGNED

- Petroria rugosa acuta* Benedetto & Herrera, 1986: 115; pl. 2, figs 1–4, 8–17 from U. San Juan Formation (M. Arenig to L. Llanvirn), Quebradas Los Gatos, San Juan Province, Argentina; also subspecies *elevata* Benedetto & Herrera, 1986: 116; pl. 2, figs 5–7, 18–19 from U. San Juan Formation (L. Llanvirn), Quebradas Ancha, San Juan Province, Argentina.



Fig. 45 *Bimuria superba* Ulrich & Cooper, 1942, from Arline Formation (Llandeilo), half mile east of Friendsville, Tennessee, USA, posterior and anterior views of the cardinal process area, based on BC 7269, $\times 6$.

Petroria rugosa Wilson, 1926: 27; pl. 5, figs 15–18 from *Orthidiella* Zone, Skoki Formation (M.–U. Arenig), Palliser Pass, British Columbia, Canada (revised Cooper 1956: pl. 221, figs 29–36).

Petroria cf. *P. austrina* of Ross & James 1987: 85; pl. 4, figs 1–5 from Shallow Bay Formation (U. Arenig), Cow Head, Newfoundland, Canada.

SPECIES TENTATIVELY ASSIGNED

Petroria ? *austrina* Ross, 1972: 27; pl. 11, figs 1–5 from bioherm of Arenig age, Meiklejohn Peak, Nevada, USA (no interiors known).

SPECIES REJECTED

Petroria lata Xu & Liu, 1984: 203; pl. 13, figs 19–26 from Dawan Formation (M.–U. Arenig), Yichang, Hubei Province, China (no platform in brachial valve, undercut cardinal process; genus uncertain but probably subfamily Chonetoideinae).

Family BIMURIIDAE Cooper, 1956

1956 Bimuriidae Cooper: 764 (pars)
1965 Bimuriidae Williams: H383 (pars)

DIAGNOSIS. Cardinal process simple, not undercut. With bema. With side septa.

REMARKS. Cooper (1956) and Williams (1965) united the two genera *Bimuria* and *Craspedelia* as the sole genera within the Bimuriidae chiefly on account of their smooth surface and side septa. However, we divide these two genera into separate families on the fundamental basis of their cardinal process. True *Bimuria* has a simple cardinal process, whilst that of *Craspedelia* (and some species formerly attributed to *Bimuria*, but attributed to the new genus *Cooperea* here) is undercut and thus assigned to the Sowerbyellidae.

GENUS ASSIGNED. *Bimuria* Ulrich & Cooper, 1942.

RANGE. Llandeilo (*B. superba*) to U. Caradoc (*B. youngiana*).

BIMURIA Ulrich & Cooper, 1942

Figs 45–47

1942 *Bimuria* Ulrich & Cooper: 622
1956 *Bimuria* Cooper: 764 pars
1965 *Bimuria* Williams: H383

TYPE SPECIES. *Bimuria superba* Ulrich & Cooper, 1942.

DIAGNOSIS. No ornament. Comae sometimes developed. Elongate and divided bema.

REMARKS. Within the species assigned to *Bimuria* by Cooper (1956) we can recognize two types, firstly a group (which includes the type species) with a simple cardinal process and elongate divided bema, and a second group, represented by *B. siphonata*, which has undercut cardinal processes and a transverse divided bema, for which we are erecting a new genus within the Craspedeliinae.

SPECIES ASSIGNED

Bimuria bugrischichiensis Severgina, in Petrunina & Severgina 1962: 91; pl. 4, figs 1, 2 from Khankharin Formation (U. Llandeilo), Uskychevka River, Gornoi Altai, USSR.

Bimuria butsi Cooper, 1956: 765; pl. 212, figs 11–31 from Little Oak Formation (U. Llandeilo–L. Caradoc), Pelham, Alabama, USA.

Christiania lamellosa Bassler, 1919: 257; pl. 49, figs 3–10 from Oranda Formation (L. Caradoc), Strasburg, Virginia, USA.

Bimuria parvula Cooper, 1956: 769; pl. 184, fig. 4; pl. 210, figs 1–4 from Chatham Hill Formation (L. Caradoc), Sharon Springs, Virginia, USA.

Bimuria peregrina Jaanusson, 1962: 5; pl. 1, figs 1–10 from Dalby Limestone (M. Caradoc), Siljan District, Sweden.

Bimuria superba Ulrich & Cooper, 1942: 623; pl. 90, figs 13–18 from Middle Arline Formation (Llandeilo), SE of Friendsville, Tennessee, USA.

Leptaena transversalis var. *youngiana* Davidson, 1871: 320; pl. 47, figs 19, 20 from Craighead Limestone (U. Caradoc), Craighead, Girvan, Scotland (revised Williams 1962: 175; pl. 16, figs 38–41; pl. 17, figs 1–3); also subspecies *recta* Williams, 1962: 175; pl. 17, figs 4–7 from Balclatchie Mudstones (L. Caradoc), Penwhapple Burn, Girvan, Scotland.



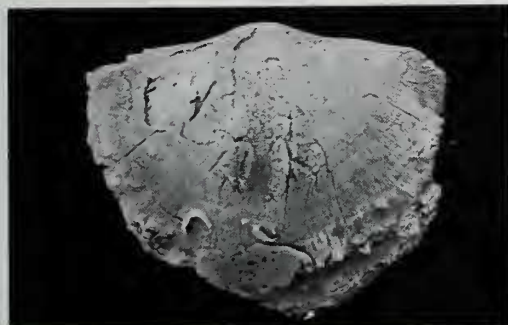
46a



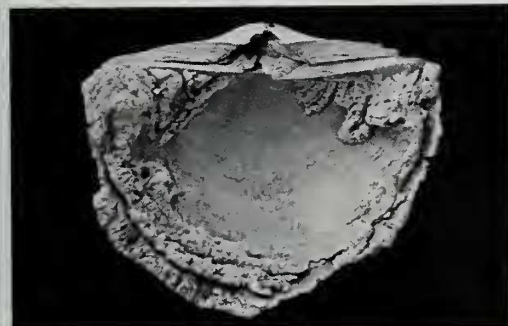
46b



46c



47a



47b

figs 46-47 *Bimuria superba* Ulrich & Cooper, 1942, from Arline Formation (Llandeilo), half mile east of Friendsville, Tennessee, USA. Fig. 46, straight down, posterior and lateral views of brachial valve interior, BC 7269, $\times 3$; Fig. 47, two views of a pair of conjoined valves showing comae, BC 7270, $\times 2$.

Bimuria triquetra Nikitin & Popov, 1984: 150; pl. 18, figs 6, 8, 11, 12 from Bestamaksкая Formation (U. Llandeilo-L. Caradoc), Novaya Archali Hill, Chinghiz Mountains, Kazakhstan, USSR.

SPECIES QUESTIONABLY ASSIGNED

Bimuria? apsaclinata Su, 1980: 273; pl. 115, figs 1-4 from Guanniaohe Formation (M. Ordovician), Lower Guanniao river, Nenjiang County, Heilongjiang Province, NE China (no interiors figured).

Bimuria dyfiensis Lockley, 1980: 215; figs 60-62, 64, 65 from Gelli-grîn Formation (U. Caradoc), Rhiw March, Llanystwmdwy, Powys, Wales (no brachial interior known).

Bimuria? matutina Cooper, 1956: 768; pl. 210, figs 6-10 from boulder in Mystic conglomerate (Llanvirn?), Stanbridge, Quebec, Canada (no interiors figured).

Bimuria sp. 1 of Cooper, 1956: 772; pl. 210, figs 12-14 from Eureka Quartzite (Llanvirn), Martins Ridge, Nevada, USA (no interior figured).

SPECIES REJECTED

Bimuria immatura Cooper, 1956: 766; pl. 211, figs 1-3 from Effna Rich Valley Formation (L. Caradoc), Porterfield Quarry, Virginia, USA (transferred to *Cooperea* gen. nov.).

Bimuria siphonata Cooper, 1956: 770; pl. 210, figs 17-24 from Pratt Ferry Formation (Llandeilo), Pratt Ferry, Alabama, USA (transferred to *Cooperea* gen. nov.).

Bimuria sp. of Liu *et al.* 1983: 277; pl. 92, fig. 17 from Tangtou Formation (L. Ashgill), Chuxian County, Anhui Province, China (probably *Christiania*).

Family SYNDIELASMATIDAE Cooper, 1956

1956 Leptestiinae Cooper: 700 *pars*

1956 Syndielasmatae Cooper: 742

1965 Isophragmatinae Williams: H375 *pars*

DIAGNOSIS. Trifid cardinal process. No bema. Side septa usually developed.

REMARKS. *Syndielasma* and *Sowerbyites* are morphologically quite close to *Isophragma* and *Taphrodonta* but differ in their possession of a trifid rather than simple cardinal process, and in having true side septa rather than a double median septum.

GENERA ASSIGNED. *Sowerbyites* Teichert, 1937; *Syndielasma* Cooper, 1956.

RANGE. Llanvirn (*Syndielasma biseptatum*) to Upper Caradoc (*Sowerbyites* spp.).

SOWERBYITES Teichert, 1937

1937 *Sowerbyites* Teichert: 66

1956 *Sowerbyites* Cooper: 723

1965 *Sowerbyites* Williams: H373

TYPE SPECIES. *Sowerbyites medioseptatus* Teichert, 1937.

DIAGNOSIS. Like *Syndielasma*, but median septum present in the brachial valve. Cardinal process fused with brachiophore bases. Side septa variably developed.

REMARKS. Only one specimen showing the interior of the brachial valve of the type species has ever been illustrated

(Teichert 1937: pl. 12, fig. 17) and thus the variability of this species is difficult to assess. That specimen shows a strong median septum which posteriorly is low and has a slight groove in its centre, and anteriorly is higher, with no groove to be seen. Of the six other species attributed by Cooper (1956) to this genus and listed below, none shows an identical septal form, although all possess a brachial valve median septum.

SPECIES ASSIGNED

Sowerbyites delicatus Cooper, 1956: 725; pl. 179, figs 7–20 from L. Sevier Shale (L. Caradoc), Athens, Tennessee, USA.

Sowerbyites gildersleevei Cooper, 1956: 725; pl. 183, figs 1–16 from Lincolnshire Limestone (U. Llandeilo), Strasburg, Virginia, USA.

Sowerbyites hami Cooper, 1956: 727; pl. 181, figs 19–33 from U. Bromide Formation (L. Caradoc), Gilsonite, Oklahoma, USA.

Sowerbyites hibernicus Mitchell, 1977: 69; pl. 12, figs 5–18 from Bardahessiagh Formation (M. Caradoc), Pomeroy, Co. Tyrone, Northern Ireland.

Sowerbyites lamellosus Cooper, 1956: 728; pl. 180, figs 17–25; pl. 181, figs 10–18; pl. 184, figs 23–27 from L. Bromide Formation (L. Caradoc), Carter County, Oklahoma, USA.

Sowerbyites [incertus] mongolicus Rozman, 1981: 129; pl. 31, figs 4–10 from Bairimski beds (U. Caradoc), Agach-Ula hills region, Mongolia (certainly *Sowerbyites*, but not a subspecies of *Titanambonites? incertus* Williams).

Sowerbyites medioseptatus Teichert, 1937: 66; pl. 12, figs 16, 17 from Upper Ordovician Limestone, Ignertoq, east coast of Melville Peninsula, Arctic Canada.

Sowerbyites subnasutus Cooper, 1956: 729; pl. 182, figs 1–11 from Lincolnshire Limestone (U. Llandeilo), Gate City, Virginia, USA.

Plectambonites triseptatus Willard, 1928: 277; pl. 2, figs 7, 8 from Holston Formation (L. Caradoc), Goodwins Ferry, New River, Virginia, USA (revised Cooper 1956: 730; pl. 169, figs 10–12; pl. 180, figs 1–13; pl. 182, figs 12–29; pl. 183, figs 17, 18; pl. 209, figs 4–7).

SPECIES REJECTED

Sowerbyites vesciseptus Percival, 1979: 106; fig. 7B.1–13 from Goonumbla Volcanics (L. Caradoc), Gunningbland, New South Wales, Australia (with bema, no side septa, transferred to *Bilobia*).

SYNDELASMA Cooper, 1956

1956 *Syndielasma* Cooper: 742

1965 *Syndielasma* Williams: H376

TYPE SPECIES. *Syndielasma biseptatum* Cooper, 1956.

DIAGNOSIS. Like *Sowerbyites* but with no median septum. Two long side septa. Cardinal process not fused anterolaterally to brachiophore bases.

REMARKS. This genus is known only from its original description by Cooper (1956), who found fourteen specimens attributable to the type species. Four brachial valve internals are illustrated by Cooper, none of which shows a median septum, although it should be remembered that the presence or absence of a median septum can be a variable feature in some plectambonitacean genera such as *Sowerbyella*.

SPECIES ASSIGNED

Syndielasma biseptatum Cooper, 1956: 734; pl. 185, figs 14–29 from Upper Pogonip Group (Llanvirn), Ikes Canyon, Nevada, USA.

Family **LEPTELLINIDAE** Ulrich & Cooper, 1936

1936 Leptellininae Ulrich & Cooper: 626 *pars*

1938 Leptellininae Ulrich & Cooper: 187 *pars*

1956 Leptellinidae Cooper: 744 *pars*

1965 Leptellinidae Williams: H376 *pars*

1965 Leptestiidae Williams: H372 *pars*

1967 Leptellinidae Havlíček: 26

1970 Leptellinidae Cocks: 155 *pars*

1984 Leptellinidae Klenina: 66

DIAGNOSIS. All with trifold cardinal process (not undercut). No side septa present. No bema present (although clear muscle bounding ridges occasionally seen).

REMARKS. This family is easily divided into two natural groups – the large group of the Leptellininae and the smaller group of the Palaeostrophomeninae in which the pedicle valve muscle field is so much more expanded and longer by comparison with the Leptellininae. It is interesting to note that the genera in the Palaeostrophomeninae have deeply impressed pallial markings: we cannot explain this.

SUBFAMILIES ASSIGNED. Leptellininae Ulrich & Cooper, 1936; Palaeostrophomeninae subfam. nov.

RANGE. Llanvirn to U. Llandovery.

Subfamily **LEPTELLININAE** Ulrich & Cooper, 1936

1936 Leptellininae Ulrich & Cooper: 626 *pars*

1956 Leptelloidinae Cooper: 763

1965 Leptellininae Williams: H376 *pars*

1970 Leptellininae Cocks: 155

DIAGNOSIS. With trifold cardinal process. Restricted pedicle valve muscle field.

REMARKS. This subfamily flourished in Middle Ordovician times, providing the dominant brachiopod species at many localities. However, the subfamily endured a cryptic extinction in the Middle Ashgill – there are no records between the Middle Ashgill *Qianjiangella* of Kazakhstan and south China and the late Llandovery records of *Merciella* in south China and the Welsh Borderland.

GENERA ASSIGNED. *Acculina* Misius, 1977; *Dulankarella* Rukavishnikova, 1956 (including *Shlyginia* Nikitin & Popov, 1983); *Kajnaria* Nikitin & Popov, 1984; *Leptellina* (*Leptellina*) Ulrich & Cooper, 1936 (including *Benignites* Havlíček, 1952, *Mabella* Klenina, 1984, *Qianjiangella* Liang, 1983 and *Urbimena* Havlíček, 1976); *Leptellina* (*Merciella*) Lamont & Gilbert, 1945; *Leptelloidea* Jones, 1928; *Reversella* Liang, 1983.

RANGE. Llanvirn (*Leptellina* spp.) to U. Llandovery (*Merciella vesper*).

ACCULINA Misius, 1977

- 977 *Acculina* Misius in Misius & Ushatinskaya: 113
 986 *Acculina* Misius: 143

TYPE SPECIES. *Acculina acculica* Misius, 1977.

DIAGNOSIS. Resupinate. Brachial valve like *Reversella*. Pedicle muscle field not enclosed anteriorly; no pedicle valve median septum.

REMARKS. Only *Acculina* and *Reversella* are resupinate within the Leptellinidae. Comparison is difficult since the type species of *Acculina* is small (maximum width 20 mm), whilst the only known species of *Reversella* is large, with valves about 50 mm wide. Although the two genera have very similar brachial valve interiors, *Reversella trigoniformis* has distinctive pedicle valve muscle bounding ridges, and so we provisionally keep the two genera distinct here; however, further work might indicate them to be congeneric. *Reversella* also has strong geniculation.

SPECIES ASSIGNED

- Acculina acculica* Misius, in Misius & Ushatinskaya 1977: 114; pl. 26, figs 21–24 from the Tabilgatinsk Formation (Middle Ordovician), northern slope of Moldo-Too mountains, northern Kirgiziya, USSR.
Acculina villosa Nikitina, 1985: pl. 1, figs 14–19 from the Rgayta Formation (Llandeilo), Talapta, southwestern Kandyktas Mountains, southern Kazakhstan, USSR.

DULANKARELLA Rukavishnikova, 1956

- 1956 *Dulankarella* Rukavishnikova: 135 *pars*
 1965 *Leptestiina* Williams: H378 *pars*
 1979 *Dulankarella* Percival: 103
 1983 *Shlyginia* Nikitin & Popov: 238
 1984 *Dulankarella* Klenina: 73

TYPE SPECIES. *Dulankarella magna* Rukavishnikova, 1956. Type species of *Shlyginia* is *Shlyginia declivis* Nikitin & Popov, 1983.

DIAGNOSIS. Normal convexity. Differs from *Leptellina* in large muscle field in pedicle valve to about half valve length or more. Adductor muscle scars usually enclosed by diductor scars in pedicle valve. Cardinal process projecting slightly or not at all posteriorly from the hinge line like *Leptellina*.

REMARKS. This genus, although erected in 1956, was essentially overlooked and unrevised until the paper by Percival (1979), although the brachial valve interior was not originally illustrated by Rukavishnikova. Nikitin & Popov (1983) erected *Shlyginia* separately from *Dulankarella* on the absence of dental plates and on a small septum or shell thickening anterior to the muscle field in the middle of the pedicle valve. Both these features are very variable in the published illustrations of both *Dulankarella* and *Shlyginia* and in any case are not features we can trust for generic differentiation (cf. *Leangella* and *Diambonia*), and we consider the two nominal genera to be the same.

SPECIES ASSIGNED

- Leptellina carinata* Yadrenkina, 1965: 12; pl. 2, figs 13–22 from Baksan Horizon, Mangazei Stage (Caradoc), Podkammenayar Tunguska River, Kuzimovk, NW Siberia, USSR.*

Shlyginia declivis Nikitin & Popov, 1983: 238; pl. 3, figs 1–5 from Andrushenskaya Formation (Caradoc), Ishim River, near Kyprianovska, Kazakhstan, USSR.

Dulankarella extraordinaria Rukavishnikova, 1956: 138; pl. 3, figs 1–3 from Dulankarinski Horizon (U. Caradoc), Degeresski beds, Kopali-Sai, Chu-Ili Mountains, Kazakhstan, USSR.

Dulankarella magna Rukavishnikova, 1956: 139; pl. 3, figs 4–9 from Otarsky Horizon (Caradoc), Dzhartas hill, Dulankara, Chu-Ili Mountains, Kazakhstan, USSR.

Dulankarella namasensis Klenina, 1984: 75; pl. 6, figs 1, 20–24 from Anderkensi Horizon (Caradoc), east of River Hamas, Chinghiz Mountains, Kazakhstan, USSR.

Shlyginia solida Nikitin & Popov, 1984: 146; pl. 16, figs 10, 12–16 from Erkebidaikski Horizon, Upper Bestamakski Formation (U. Llandeilo–basal Caradoc), Chagan River, Chinghiz Mountains, Kazakhstan, USSR.

Dulankarella subquadrata Klenina, 1984: 76; pl. 6, figs 3, 12, 13, 16, 18, 19, 25 from Anderkensi Horizon (Caradoc), east of River Hamas, Chinghiz Mountains, Kazakhstan, USSR (probably a synonym of *D. namasensis*).

SPECIES REJECTED

Dulankarella fragilis Rukavishnikova: 136; pl. 2, figs 15–22 from the Anderkensi horizon (Caradoc), Kopali-sai, Chu-Ili Mountains, Kazakhstan, USSR. (Nikitin & Popov (1983: 237) appear wrong to attribute this species to *Shlyginia*, since pl. 2, figs 19–21 of Rukavishnikova 1956 show that *S. fragilis* possesses a bema; however, the interior of Rukavishnikova's holotype (1956: pl. 2, fig. 15) is unknown and more than one species may be involved).

Dulankarella ? partita Percival, 1979: 103; figs 5C.1–7, 6 from Goonumbla Volcanics (U. Caradoc), Gunningbland, New South Wales, Australia (the cardinalia is not leptellinid and is similar to *Sowerbyites*).

KAJNARIA Nikitin & Popov, 1984

- 1984 *Kajnaria* Nikitin & Popov: 144

TYPE SPECIES. *Kajnaria derupta* Nikitin & Popov, 1984.

DIAGNOSIS. Strong muscle bounding ridges in pedicle valve, with anteriorly to them two curved ridges (the 'diaphragm' of Nikitin & Popov 1984). Variably developed pedicle valve myophragm.

REMARKS. Within the Plectambonitacea we have not seen elsewhere any structure exactly like that in the pedicle valve of *Kajnaria*. Its function is unknown, it is certainly not part of the muscle field and in the two shells illustrated (Nikitin & Popov 1984: pl. 18, figs 14, 15) it varies in the completion anteriorly of the curved ridge. The genus is assigned to the Leptellininae because of the internal structure of the brachial valve, which is similar to *Leptellina*.

SPECIES ASSIGNED

- Kajnaria derupta* Nikitin & Popov, 1984: 145; pl. 18, figs 10, 13–16 from Bed bs_{iii}, U. Bestamakskaya Formation, Erkebidaikski horizon (M. Ordovician), south of New Archal Hill, Chinghiz Mountains, Kazakhstan, USSR.

LEPTELLINA (LEPTELLINA) Ulrich & Cooper, 1936
Figs 48, 49

- 1936 *Leptellina* Ulrich & Cooper: 626
 1938 *Leptellina* Ulrich & Cooper: 190

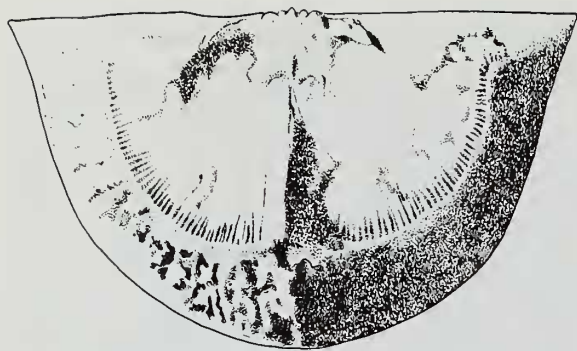


Fig. 48 *Leptellina (Leptellina) tennesseensis* Ulrich & Cooper, 1936, from Lenoir Formation (Llandeilo), quarter mile west of Friendsville, Tennessee, USA, interior of brachial valve, based on BB 1228, $\times 5$.

- 1952 *Benignites* Havlíček: 13
 1965 *Leptellina* Williams: H376
 1965 *Merciella* Williams: H376 pars
 1967 *Leptellina* Havlíček: 27 pars
 1976 *Urbimena* Havlíček: 367
 1976 *Benignites* Havlíček: 368
 1983 *Qianjiangella* Liang in Liu *et al.*: 274
 1984 *Leptellina (Mabella)* Klenina: 69

TYPE SPECIES. *Leptellina tennesseensis* Ulrich & Cooper, 1936. Type species of *Benignites* is *Strophomena primula* Barrande, 1879; of *Mabella* is *Leptellina (Mabella) semiovalis* Klenina, 1984; of *Qianjiangella* is *Q. qianjiangensis* Liang, 1983 and of *Urbimena* is *U. mareki* Havlíček, 1976.

DIAGNOSIS. Normal convexity. With platform. Pedicle valve muscle field small (usually less than quarter valve length). Thin central ridge to cardinal process with lateral components less prominent (only thin central process projecting posteriorly from hinge line, and even this is sometimes entirely anterior to the hinge line).

REMARKS. The muscle field in the pedicle valve shows some variation. In most species, including the type species, it is small and does not extend more than a quarter of the valve length, and the adductor scars are usually open anteriorly. However, in *L. (Merciella)* the adductor scars are enclosed anteriorly by the diductor scars. This genus was very common in Llanvirn to Ashgill times, and in many cases dominated the community in which it occurred. Further research might recognize more features worthy of subgeneric recognition, but we have been unable to recognize any (apart from those of *Merciella*), and so we group here all the species hitherto attributed to *Leptellina*, *Benignites*, *Mabella*, *Qianjiangella* and *Urbimena* into a single undivided *Leptellina (Leptellina)*. *Benignites* is said by Havlíček (1976: 368) to differ from *Leptellina* 'in having a slender adductor scar narrowing to the front of the ventral muscle field', but we do not think this important, and indeed the muscle scars of *Leptellina* are very variable and include 'Benignites'-like forms. The perforated platform margin is also sometimes continuous, and other plectambonitaceans, such as *Merciella*, also show this occasionally (Cocks 1970: pl. 1, figs 2, 4).

According to Havlíček (1976: 367), *Urbimena* differs from *Leptellina* in lacking dental plates, in having a very narrow adductor scar in the pedicle muscle field and in having a very weak 'submarginal rim' (what we would term a platform) in the brachial valve. In fact there are weak dental plates in

Urbimena (Havlíček 1976: pl. 1, fig. 2), the narrow adductor scar is a variably developed feature in all plectambonitaceans, and the weakness of the platform is merely because the specimens of *U. mareki* are all very small (less than 8 mm wide). We consider the two genera as synonyms. It is true that the strength of the platform is very much weaker in the type species of *Benignites* and *Urbimena* than in other species of *Leptellina*, but we have seen all intergrades between a barely continuous row of septules and a very strong platform and we cannot therefore separate these genera on that criterion. When Klenina (1984) erected *Mabella* she did it on the basis of the forked anterior end of the brachial valve median septum. This is a common phenomenon within the Leptellininae and other members of the Plectambonitacea and is simply a median modification of the platform which forms the septum: for example, it is seen in *Merciella striata* (Rong & Yang 1981: pl. 2, figs 4, 5) and in *Leptellina pulchra* Cooper (1956: pl. 189, figs 21–23). Otherwise *Mabella* is similar to *Qianjiangella* and the two are placed in synonymy here with *Leptellina*.

SPECIES ASSIGNED

- Leptellina bella* Cooper, 1956: 748; pl. 186, figs 1–8; pl. 190, figs 1–4 from Whitesburg Formation (L. Caradoc), Bulls Gap, Tennessee, USA.
Leptellina deminuta Liu, 1976: 147; pl. 2, figs 20–23 from Jiacun Group (Llanvirn–Llandeilo), Mount Jolmo Lungma area, Tibet, China.
Leptellina kirgizica Misius, 1986: 140; pl. 11, figs 29–36; pl. 12, figs 1–10 from M. Tabulgat Formation (U. Llandeilo–L. Caradoc), R. Tabulgat, Moldo-Too, Kirgiziya, USSR.
Leptaena llandeiloensis Davidson, 1883: 171; pl. 12, fig. 26, non figs 27–29 from L. Ardwell Mudstone (M. Caradoc), Ardmillan Braes, Girvan, Scotland (revised Williams 1962: 164; pl. 15, figs 27–29, 32).
Urbimena mareki Havlíček, 1976: 368; pl. 1, figs 1–6 from Libeň Formation (L. Caradoc), Motol, Prague, Czechoslovakia (but his pl. 1, fig. 4 may not be the same species).
Leptelloidea multicostata Rukavishnikova, 1956: 132; pl. 2, figs 8–11 from Otarski Horizon (Caradoc), Bokkot River, Chu-Ili Mountains, Kazakhstan, USSR (revised Misius 1986: 133; pl. 12, figs 11–30; pl. 13, figs 1, 2).
Leptellina (Mabella) obtusa Klenina, 1984: 71; pl. 5, figs 5, 6; pl. 6, fig. 2 from Taldiboiskaya Formation (Ashgill), River Taldiboi, Chinghiz Mountains, Kazakhstan, USSR (same locality and horizon as *M. semiov* and may be a synonym).
Leptellina occidentalis Ulrich & Cooper, 1938: 191; pl. 39, figs 3, 7 from Upper Pogonip Formation (Llanvirn), Ikes Canyon, Nevada, USA.
Leptellina primaria Cooper, 1956: 752; pl. 187, figs 1–7 from Crown Point Formation (Llanvirn–Llandeilo), Valcour Island, Lake Champlain, New York, USA.
Strophomena primula Barrande, 1879: pl. 52, fig. 3 from the Dobrotivá Shales (Llandeilo), Svata Dobrotivá, Czechoslovakia (revised Havlíček 1967: 27; pl. 1, figs 9–13).
Leptellina pulchra Cooper, 1956: 753; pl. 189, figs 1–23; pl. 195, figs 9–16; pl. 219, fig. 14 from Effna–Rich Valley Formations (Llandeilo), Porterfield Quarry, Virginia, USA.
Qianjiangella qianjiangensis Liang, in Liu *et al.* 1983: 275; pl. 95, figs 5–8 from Changwu Formation (M. Ashgill), Jianglütang village, Chunan County, W. Zhejiang, China.
Leptellina rhacta Williams, 1962: 164; pl. 15, figs 17–19, 21,

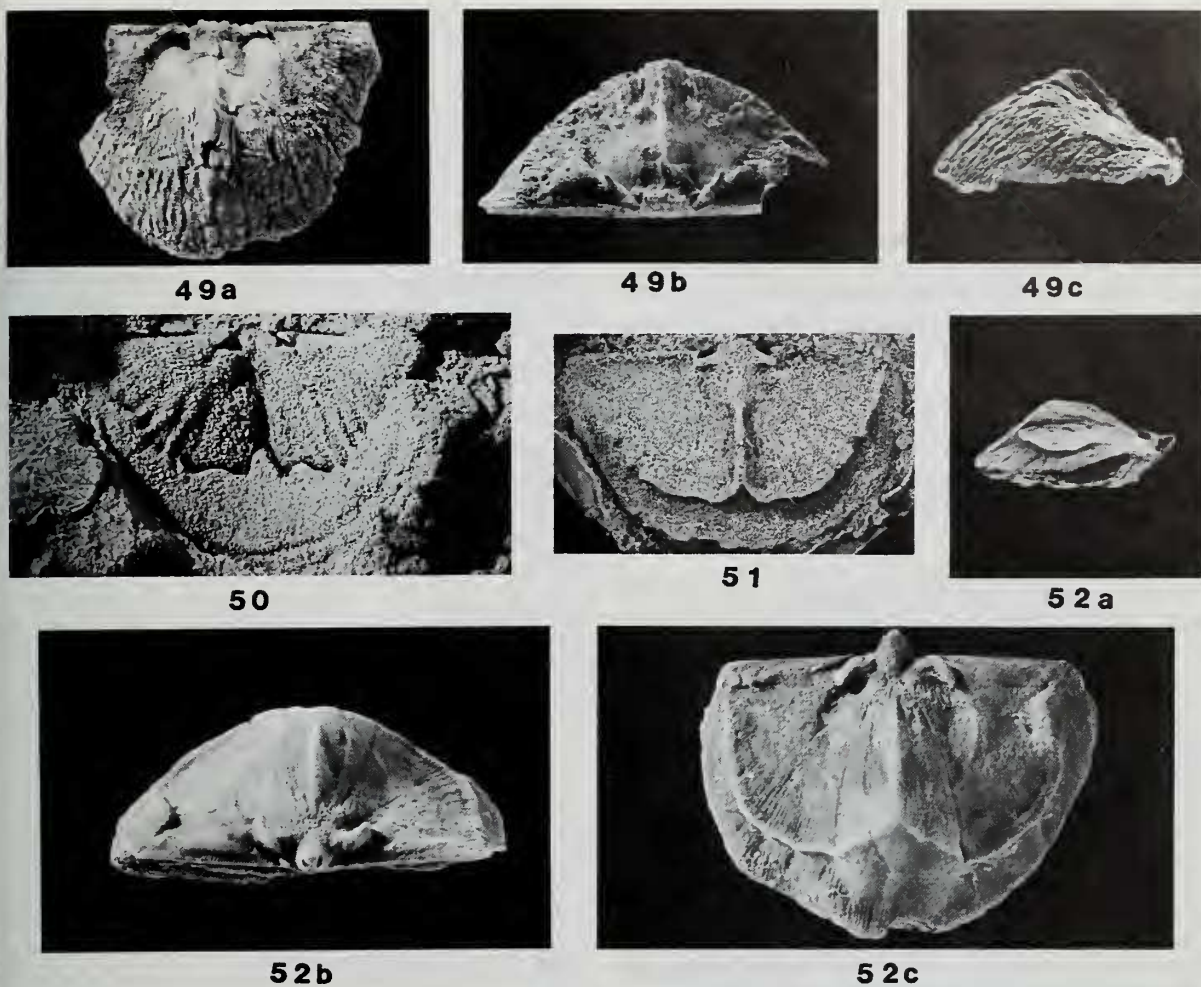


Fig. 49 *Leptellina (Leptellina) tennesseensis* Ulrich & Cooper, 1936, from Lenoir Formation (Llandeilo), quarter mile west of Friendsville, Tennessee, USA, downwards, posterior and lateral views of a brachial valve interior, BB 1228, $\times 4$.
 Figs 50, 51 *Leptellina (Merciella) vesper* (Lamont & Gilbert, 1945), from Wych Beds (U. Llandovery), Coneygore Coppice, near Alfrick, Worcestershire, England. Fig. 50, natural internal mould of brachial valve, BU 370, $\times 3$; Fig. 51, latex cast of brachial valve interior, lectotype, the original of Lamont & Gilbert 1945: pl. 4, figs 10, 12, BU 369, $\times 3$.
 Fig. 52 *Leptelloidea leptelloides* (Bekker, 1922), topotype from Kukruse Formation (L. Caradoc), Kohhla-Järve, Estonia, USSR, lateral, posterior and downward views of the interior of a brachial valve, BB 5169; 52a, $\times 3$; 52b, c, $\times 5$.

22 from U. Stinchar Limestone (Llandeilo), Brockloch, Girvan, Scotland.

Leptellina seletensis Nikitin & Popov, 1983: 235; pl. 3, figs 6, 9, 11, 13–15 from Isobilnaya Formation, Tselinogradski Horizon (Middle Ordovician), Akzhar River basin, central Kazakhstan, USSR.

Leptellina semilunata Rozman, 1981 (*non* Williams, 1962): 132; pl. 24, figs 16–23 from *Christiania subquadrata* beds (Llandeilo), Agach-Ula, S. Mongolian Altai, Mongolia (same genus as *L. semilunata*, but different ornament).

Leptellina semilunata Williams, 1962: 164; pl. 15, figs 23–26 from Stinchar Limestone (Llandeilo), Brockloch, Girvan, Scotland.

Leptellina (Mabella) semiovalis Klenina, 1984: 69; pl. 5, figs 1, 3, 4; pl. 9, figs 4, 7 from Taldiboiskaya Formation (Ashgill), River Taldiboi, Chinghiz Mountains, Kazakhstan, USSR.

Leptella sinensis Xu, Rong & Liu, 1974: 152; pl. 66, figs 13, 17, 18 from Shihtzipu Formation (Llandeilo), Zunyi, Zunyi County, N. Guizhou, China.

Leptellina subcarinata Cooper, 1956: 754; pl. 190, figs 32–39 from Athens Formation (Llandeilo), Riceville, Tennessee, USA.

Leptellina sublamellosa Cooper, 1956: 755; pl. 188, figs 12, 15–24; pl. 190, figs 5–25 from Chatham Hill Formation (Llandeilo), Sharon Springs, Virginia, USA.

Leptellina tabylgatyensis Misius, 1986: 137; pl. 11, figs 1–28 from Tabulgat Formation (L. Caradoc), River Tabulgat, Moldo-Too, north Kirgiziya, USSR.

Leptellina tennesseensis Ulrich & Cooper, 1936: 626 (illustrated in Ulrich & Cooper, 1938: pl. 39, figs 1, 2, 4, 5) from the Lenoir Formation (Llandeilo), Friendsville, Tennessee, USA.

Leptellina transversa Cooper, 1956: 758; pl. 191, figs 1–8 from Arline Formation (Llanvirn–Llandeilo), Porterfield, Virginia, USA.

Leptellina sp. of Williams 1962: 167; pl. 16, figs 1, 2 from Balclatchie Conglomerate (L. Caradoc), Penwhapple Burn, Girvan, Scotland.

SPECIES QUESTIONABLY ASSIGNED

Leptellina abbreviata Cooper, 1956: 747; pl. 191, figs 23–31 from Oranda Formation (Llandeilo), Strasburg, Virginia, USA (pedicle valves look similar, but no brachial valve interiors figured).

Leptaena decipiens Billings, 1865: 74, fig 67 (reillustrated by Ulrich & Cooper, 1938: pl. 39, figs 13–15) from Limestone in Lévis Shale (Arenig), Lévis, Quebec, Canada (pedicle valves look similar, but no brachial valves now known).

Plectambonites delicatula Butts, 1926: 116; pl. 26, figs 20, 21 (also Cooper 1956: pl. 188, figs 13, 14; pl. 191, figs 32–39) from Little Oak Formation (Llandeilo), Pelham, Alabama, USA (pedicle valve looks similar, but no brachial valve interiors figured).

Sampo (Leptellina) elevata Spjeldnaes, 1957: 73; pl. 6, figs 11, 12 from 4b beds (M. Caradoc), Gomnes-Rud, Ringerike, Norway (no brachial interiors figured).

Leptellina huanghuensis Chang, 1983: 476; pl. 1, fig. 1 from Miaopo Formation (U. Llandeilo–L. Caradoc), Huanghuachang, Yichang County, Hubei Province, China (no interiors known).

Leptellina incompta Cooper, 1956: 750; pl. 191, figs 9–22 from shale below Eureka Quartzite (Llanvirn?), Martins Ridge, Monitor Range, Nevada, USA (pedicle valve unlike *Leptellina*; brachial valve not figured in posterior region).

Leptellina (Mabella) incurvata Klenina, 1984: 72; pl. 5, fig. 2 from Taldiboisikaya Formation (Ashgill), River Taldiboi, Chinghiz Mountains, Kazakhstan, USSR (same locality and horizon as *M. semiovalis* but no interiors known).

Leptellina (Leptellina) infrequens Klenina, 1984: 68; pl. 7, fig. 1; pl. 8, fig. 7; pl. 9, fig. 5 from Abaevskaya Formation (Llanvirn–Llandeilo), SE Ordatas Hill, Pre-Chinghiz Mountains, Kazakhstan, USSR (no interiors illustrated).

Leptaena? ledetensis Reed, 1906: 54; pl. 4, figs 39–41 from Naunkangyi Formation (?L. Caradoc), Ledet, northern Shan States, Burma (no brachial valve interior figured, but pedicle valve with platform, cardinal process trifid).

Leptellina maxima Zhang, 1981: 89; pl. 40, figs 9, 10 from L. Kiziltseika Formation (Ashgill), Jaboshaer, Fuyun County, Xinjiang Province, China (no interiors figured).

Leptellina platys Cooper, 1956: 751; pl. 186, figs 13, 14 from Benbolt Formation (L. Caradoc), Clinchport, Virginia, USA (no interiors known).

Orthis? productoides McCoy, 1846: 32; pl. 3, fig. 15 (*non O. productoides* Murchison, 1840) from Tramore Limestone (Caradoc), Tramore, Co. Waterford, Ireland (discussed Cocks 1978: 93, no interior figured).

Leptellina sanyuanzhensis Liu, in Liu *et al.* 1983: 273; pl. 93, figs 1–5 from Tangtou Formation (L. Ashgill), Chuxian County, Anhui Province, China (interiors poorly figured).

SPECIES REJECTED

Leptellina carinata Yadrenkina, 1965: 12; pl. 2, figs 13–22 from Baksan Horizon, Mangazei Stage (Caradoc), Podkamennaya Tunguska River, Kuzimovk, NW Siberia, USSR (large pedicle valve muscle field, so assigned to *Dulankarella*).

Benignites (Leptestiina) prantli Havlíček, 1952: 412 from Králův Dvůr Shales (Ashgill) of Králův Dvůr, Czechoslovakia (the type of *Leptestiina* – now a separate genus).

Leptellina sp. 1 of Cooper 1956: 759; pl. 187, fig. 8 from Edinburg Formation (Llandeilo), Strasburg, Virginia, USA (overhanging cardinal process).

LEPTELLINA (MERCIELLA) Lamont & Gilbert, 1945
Figs 50, 51

- 1945 *Leptella (Merciella)* Lamont & Gilbert: 655 *pars*
1965 *Merciella* Williams: H376 *pars*
1970 *Merciella* Cocks: 155
1981 *Merciella* Rong & Yang: 170

TYPE SPECIES. *Leptella (Merciella) vesper* Lamont & Gilbert, 1945.

DIAGNOSIS. Differs from *Leptellina (Leptellina)* in having a broader cardinal process, and in having a more elevated bema.

REMARKS. This is the only known Silurian representative of the Leptellinac. There is a gap in the stratigraphical record between the middle Ashgill records of *Leptellina (Leptellina)* and the late Llandovery records of *Leptellina (Merciella)*. However, there is no doubt that the nominal genera are very close in morphology, which is why *Merciella* is relegated here to its original subgeneric status (although of course within a different genus).

SPECIES ASSIGNED

- Merciella striata* Rong, Xu & Yang, 1974: 198; pl. 93, figs 9, 10 from Lojoping Formation (U. Llandovery), Dazhongba, Yichang, W. Hubei, China.
Leptella (Merciella) vesper Lamont & Gilbert, 1945: 655; pl. 4, figs 7–12 from Wych Formation (Upper Llandovery), Alfrick, Worcestershire, England.

LEPTELLOIDEA Jones, 1928
Figs 52, 53

- 1928 *Leptelloidea* Jones: 475
1930 *Leptelloidea* Öpik: 133
1933 *Leptelloidea* Öpik: 30
1956 *Leptelloidea* Cooper: 763
1965 *Leptelloidea* Williams: H376

TYPE SPECIES. *Plectambonites schmidti* var. *leptelloides* Bekker, 1922.

DIAGNOSIS. Normal convexity, large strong cardinal process projecting posteriorly from hinge line, but cardinal process separate from socket plates. Large pedicle valve muscle scars extending to about half valve length (much longer than in *Leptellina* but not so wide as in *Dulankarella*): adductor scars enclosed by diductor scars. Distinctive articulation including pits and accessory teeth in the ends of the dental plates and corresponding structures in brachial valve.

REMARKS. Some specimens from the Lower Meitan Formation (L. Arenig) of SW China were identified and illustrated as *Leptelloidea leptelloides* (e.g. Wang *et al.* 1964: 181; pl. 26, figs 4–8), but these are now known to lack a cardinal process and have been reassigned to *Leptella grandis* (Xu *et al.* 1974: 149; pl. 65, figs 14–17). Despite the many nominal species at one time or another attributed to *Leptelloidea*, the distinctive articulation and musculature of *L. leptelloides* itself makes us place it as the only species within the genus.

SPECIES ASSIGNED

- Plectambonites leptelloides* Bekker, 1922: 68; pl. 3, fig. 16; pl. 4, fig. 12; pl. 5, figs 9–13 from Kukruse Formation (L. Caradoc), Kohtla-Järve, Estonia, USSR.

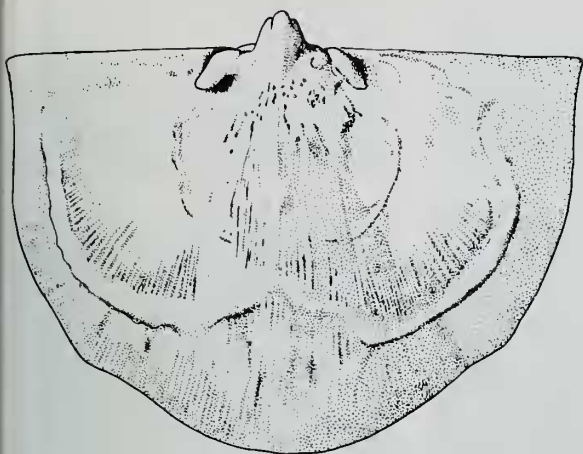


Fig. 53 *Leptelloidea leptelloides* (Bekker, 1922), from Kukruse Formation (L. Caradoc), Kohtla-Järve, Estonia, USSR, interior of brachial valve, based on BB 5169, $\times 6$.

SPECIES QUESTIONABLY ASSIGNED

eptelloidea campestris Reed, 1936: 42; pl. 3, figs 16, 17 from Naunkangyi Formation (?L. Caradoc), west of Yeosin, southern Shan States, Burma (no pedicle valve interior figured, so uncertain whether *Leptelloidea* or *Leptellina*, but brachial valve typical).

eptelloidea (*Benignites*?) *heintzi* Spjeldnaes, 1957: 74; pl. 4, figs 10–11 from 4aa Beds (Llanvirn), Ravaldsjølven, Sandsvaer, Norway (no brachial interiors known).

eptelloidea yaxianensis Xu & Su, 1979: 108 from Middle Ordovician iron ores, Yaxian county, Hainan Island, China (brachial valve interior uncertain).

eptelloidea yeosinensis Reed, 1932b: 196; pl. 3, figs 3–6 from Pindaya Formation (Caradoc?), Yeosin, southern Shan States, Burma (no pedicle valve interior figured, so uncertain whether *Leptelloidea* or *Leptellina*, but brachial valve typical).

SPECIES REJECTED

eptelloidea derfelensis Jones, 1928: 479; pl. 25, figs 3–7 from Derfel Limestone (L. Caradoc), Nant Aber Derfel, Gwynedd, Wales (transferred to *Leptestiina* by Williams 1963: 430).

eptelloidea multicostata [Borrissiak MS] Rukavishnikova, 1956: 132; pl. 2, figs 8–11 from Otarsky Horizon (Caradoc), Bokkot River, Chu-Ili Mountains, Kazakhstan, USSR (transferred to *Mabella* by Klenina 1984: 72).

eptelloidea musca Öpik, 1930: 140; pl. 8, figs 95, 97–108 and subspecies *alata* Öpik, 1930: 144; pl. 8, fig. 96 both from Kukruse Formation (L. Caradoc), Kohtla-Järve, Estonia, USSR (transferred to *Bilobia* by Cooper 1956: 761; pl. 192, figs 21–24).

eptelloidea rosendahli Spjeldnaes, 1957: 75; pl. 2, figs 4–5 from Coelosphaeridium Beds (M. Caradoc), Fangberget, Ringsaker, Norway (to *Bilobia*).

eptelloidea sholeshookensis Jones, 1928: 488; pl. 25, fig. 19 from Slade and Redhill Mudstone Formation (M. Ashgill), Lower Cresswell, Dyfed, Wales (transferred to *Leangella*? by Cocks 1978: 96).

eptelloidea subquadrata Rukavishnikova, 1956: 134; pl. 2, figs 12–14 from Kopalinski Horizon (Llanvirn), Kstau-sai, Chu-Ili Mountains, Kazakhstan, USSR (uncertain genus but Rukavishnikova 1956: 135 compares the species with *Bilobia musca* and *Leangella scissa*).

REVERSELLA Liang, 1983

1983 *Reversella* Liang in Liu *et al.*: 274

TYPE SPECIES. *Reversella trigoniformis* Liang, 1983.

DIAGNOSIS. Resupinate and strongly geniculate. Brachial valve like *Acculina*. Pedicle muscle field with strong bounding ridges, meeting anteriorly, and with central strong myophragm within the muscle field.

REMARKS. *Reversella* is close to *Acculina*, but its large valves show strong geniculation by comparison with *Acculina*, which lacks geniculation and in addition has the muscle bounding ridges in the pedicle valve.

SPECIES ASSIGNED

Reversella trigoniformis Liang, in Liu *et al.* 1983: 274; pl. 98, figs 1–5 from Changwu Formation (M. Ashgill), Jianglütang, Chunan County, W. Zhejiang, China.

Subfamily PALAEOSTROPHOMENINAE nov.

DIAGNOSIS. With trifid cardinal process. Large open pedicle valve muscle field. Usually with deeply impressed pallial markings in both valves.

REMARKS. This group of plectambonitaceans, which are often of very large size for the superfamily and confused in early works with strophomenaceans, has been classified in different families and subfamilies in the past. In fact the genera below form a close-knit group, which has caused us to suppress *Titanambonites* and *Ishimia* in favour of *Apatomorpha* and *Toquimia* respectively. The subfamily is included within the Leptellinidae on the basis of the trifid cardinal processes, which are not undercut, and on the lack of bema or side septa.

GENERA ASSIGNED. *Apatomorpha* Cooper, 1956 (including *Titanambonites* Cooper, 1956); *Glyptambonites* Cooper, 1956; *Palaeostrophomena* Holtedah, 1916; *Toquimia* Ulrich & Cooper, 1936 (including *Ishimia* Nikitin, 1974).

RANGE. Llanvirn (*Toquimia kirki*) to U. Caradoc (*Toquimia sumsarica*).

APATOMORPHA Cooper, 1956

- 1956 *Apatomorpha* Cooper: 709
 1956 *Titanambonites* Cooper: 717
 1963 *Titanambonites* Williams: 160
 1965 *Apatomorpha* Williams: H373
 1965 *Titanambonites* Williams: H375

TYPE SPECIES. *Rafinesquina pulchella* Raymond, 1928.
 Type species of *Titanambonites* is *T. medius* Cooper, 1956.

DIAGNOSIS. Brachial valve like *Glyptambonites* but pedicle valve differs in wider muscle field with shorter muscle bounding ridges. No platform.

REMARKS. We can find no substantial differences between *Apatomorpha* and *Titanambonites* except that of size, and described but not illustrated differences in the articulation, both of which are regarded here as intrageneric variation. *Glyptambonites* is also very similar (see below), but still regarded as separate in this paper.

SPECIES ASSIGNED

- Plectambonites amplus* Raymond, 1928: 297; pl. 2, fig 9; pl. 3, fig. 12 from Lenoir Formation (U. Llandeilo), 6 miles SE of Knoxville, Tennessee, USA (revised Cooper 1956: 718; pl. 177 &c.).
Titanambonites medius Cooper, 1956: 721; pl. 178, figs 9–21; pl. 185, figs 11–15 from base of Athens Formation (U. Llandeilo–L. Caradoc), Christiansburg, Tennessee, USA.
Titanambonites praecursor Cooper, 1956: 722; pl. 184, figs 6–12 from the Lenoir Formation (Llandeilo), Friendsville, Tennessee, USA.
Rafinesquina pulchella Raymond, 1928: 296; pl. 3, fig. 10 from Athens Formation (U. Llandeilo–L. Caradoc), Tennessee, USA (revised Cooper 1956: 709; pl. 166, figs 1–20).

SPECIES QUESTIONABLY ASSIGNED

- Titanambonites convexus* Cooper: 719; pl. 178, figs 1–8 from Little Oak Formation (Llandeilo–Caradoc), Newhope, Alabama, USA (brachial interior not known).
Titanambonites sp. 1 of Cooper, 1956: 723; pl. 177, fig. 11 from Lenoir Formation (Llandeilo), Pratt Ferry, Alabama, USA (no interior known).

SPECIES REJECTED

- Apatomorpha altaicus* Severgina, 1960: 406; pl. 0–17, figs 19–21 from Khankharin Formation (U. Llandeilo), River Ebogon, Gornoi Altai, USSR (with platform, so to *Toquimia*).
Titanambonites incertus Williams, 1962: 160; pl. 14, figs 36–38; pl. 15, figs 1–4, 6 from Balclatchie Mudstones (L. Caradoc), Girvan, Scotland (genus uncertain: pedicle valve with inclined dental plates like a leptellinid, brachial valve interior not well known).
Titanambonites magnus Nikitin, 1974: 56; pl. 5, figs 1–5 from Andryshenskaya Formation (U. Llanvirn?), Ishim River, Kazakhstan, USSR (with platform, transferred to *Toquimia*).
Titanambonites planus Rozman, 1964: 148; pl. 13, figs 1–7 from U. Kalychan Formation (M. Ordovician), River Kalychan, Seleniakh Mountains, NE USSR (platform present, so assigned to *Toquimia*).

GLYPTAMBONITES Cooper, 1956

Figs 54–56

- 1956 *Glyptambonites* Cooper: 712
 1965 *Glyptambonites* Williams: H373

TYPE SPECIES. *Glyptambonites musculosus* Cooper, 1956.

DIAGNOSIS. No platform seen (although no entire brachial valve yet illustrated). Like *Apatomorpha* but with pedicle valve muscle field narrower and with longer muscle bounding ridges.

REMARKS. *Glyptambonites* is extremely close in morphology to *Apatomorpha* (and its synonym *Titanambonites*), differing generically in our view only in the relative narrowness of the pedicle valve muscle field and perhaps also the longer bounding ridges of the two pedicle valves of *G. musculosus* yet illustrated. Other species of *Glyptambonites* assigned by Cooper (1956), e.g. *G. glyptus*, have wider and shorter muscle bounding ridges and delicate cardinal processes when compared with the bulbous process of *G. musculosus*, and may thus belong to a separate taxon, perhaps a subgenus. The rugae and concentric ornament seen variably in *G. musculosus* and other species are not, in our view, helpful in generic differentiation.

SPECIES ASSIGNED

- Glyptambonites musculosus* Cooper, 1956: 715; pl. 171, fig. 15; pl. 175, figs 9–13; pl. 176, figs 1–5 from Oranda Formation (L. Caradoc), Linville Station, Virginia, USA.

SPECIES QUESTIONABLY ASSIGNED

- Glyptambonites glyptus* Cooper, 1956: 713; pl. 168, figs 1, 2; pl. 173, figs 13–23; pl. 175, figs 1–8 from Effna–Rich Valley Formation (L. Caradoc), Porterfield Quarry, Virginia, USA.
Glyptambonites aff. *glyptus* Cooper; Williams, 1962: 160; pl. 14, figs 33–35 from Lower Stinchar Limestone (Llanvirn–Llandeilo), Tormitchell, Girvan, Scotland.
Sowerbyella platys Butts, 1940: 200; 1942: 109; pl. 95, fig. 17 probably from Edinburg Formation (L. Caradoc), Strasburg, Virginia (see Cooper, 1956: 716).

PALAEOSTROPHOMENA Holvedahl, 1916

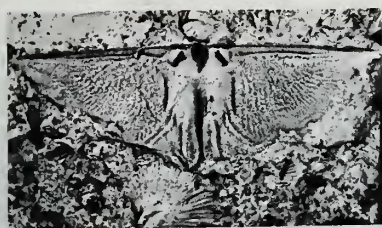
Figs 57, 58

- 1916 *Palaeostrophomena* Holvedahl: 43
 non 1932 *Palaeostrophomena* Öpik: 35 (rejected by Öpik, 1933)
 1933 *Palaeostrophomena* Öpik: 24
 1956 *Palaeostrophomena* Cooper: 700
 1965 *Palaeostrophomena* Williams: H373

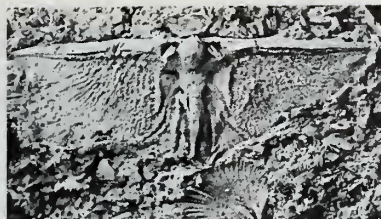
TYPE SPECIES. *Strophomena concava* Schmidt, 1858.

DIAGNOSIS. Resupinate.

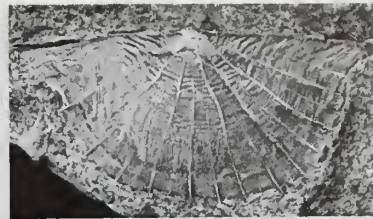
REMARKS. No brachial valve interiors of *P. concava* are known although from Öpik's (1933: pl. 4, fig. 1) illustration of the exterior, it is certain that the cardinal process is trifid. It is the only member of the subfamily which is resupinate. None of the North American species described by Cooper (1956), which are listed below, possess a platform, and a new genus would be required for them if a platform was subsequently discovered in *P. concava*. All the North American specimens are resupinate and also possess a trifid cardinal process.



54a



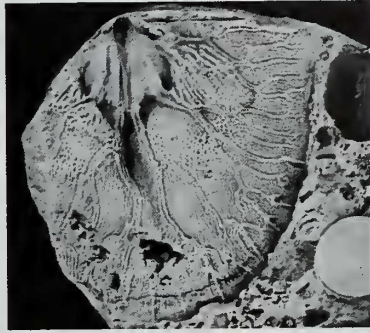
54b



55



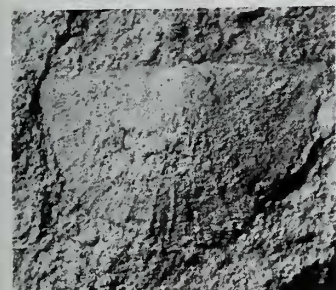
56



57



58



59



60



61

- Fig. 54 *Glyptambonites musculosus* Cooper, 1956, paratype from Oranda Formation (L. Caradoc), 0.6 miles NW of Linville Station, Virginia, USA, natural internal mould of brachial valve and latex cast of it, the original of Cooper 1956: pl. 176, figs 4, 5, USNM 117388c, $\times 2$.
- Figs 55, 56 *Glyptambonites* sp. from Balclatchie Mudstones (L. Caradoc), Penwhapple, Girvan, Strathclyde, Scotland, the originals of Williams 1962: pl. 14, figs 25, 31. Fig. 55, pedicle valve exterior, BB 15140, $\times 3$; Fig. 56, internal mould of brachial valve, BB 15141, $\times 3$.
- Figs 57, 58 *Palaeostrophomena kilbuchoensis* (Davidson, 1883), from beds of Caradoc age, near Kilbucho Church, 3 km west of Cutler, Peebleshire, Scotland. Fig. 57, natural internal mould of brachial valve, the original of Davidson 1883: pl. 13, fig. 2, GSE 6625, $\times 3$; Fig. 58, natural internal mould of pedicle valve, the original of Davidson 1883: pl. 13, fig. 1, lectotype selected Cocks 1978: 92, GSE 359, $\times 2$.
- Figs 59–61 *Toquimia aranea* (Salter, 1865), from Lower Ordovician beds, Niti, NW India. Fig. 59, partly exfoliated pedicle valve exterior from Damchen, B 4102, $\times 2$; Fig. 60, natural internal mould of pedicle valve from Upper Rimkin, the original of Salter in Salter & Blanford 1865: pl. 3, fig. 11, and selected here as the **lectotype** of *Strophomena nubigena* Salter, B 15804, $\times 1.5$; Fig. 61, natural internal mould of brachial valve from Damchen, the original of Salter in Salter & Blanford 1865: pl. 3, fig. 10 (right) and selected here as the **lectotype** of *Strophomena aranea* Salter, BC 10606, $\times 1.5$.

SPECIES ASSIGNED

- Palaeostrophomena angulata* Cooper, 1956: 702; pl. 168, figs 3–10; pl. 194, figs 19–22 from the Botetourt Formation (L. Caradoc), Catawba, Virginia, USA.
- Palaeostrophomena canalis* Lockley, 1980: 210; figs 47–52 from Gelli-grin Formation (U. Caradoc), Gelli-grin, Powys, Wales.
- Strophomena concava* Schmidt, 1858: 215 from Uhaku Formation (Llandeilo), Ärra, Estonia, USSR (revised Öpik, 1933: 25; pl. 2, figs 1–4; pl. 3, fig. 1; pl. 4, fig. 1; pl. 8, fig. 2).
- Orthis* vel *Strophomena*? *kilbuchoensis* Davidson, 1883: pl. 13, figs 1, 2 from beds of Caradoc age, Kilbucho, Peebleshire, Scotland (revised Williams 1962: 157; pl. 14, figs 22–25, 27, 28, 31).

- Palaeostrophomena magnifica* Williams in Whittington & Williams 1955: 414; pl. 39, figs 64–70 from Derfel Limestone (L. Caradoc), Pont Aberderfel, Gwynedd, Wales.
- Palaeostrophomena necopina* Popov, 1980b: 145; pl. 1, figs 8–11 from Anderkanski Horizon (U. Llandeilo–L. Caradoc), Katnak Mountain, Chu-Ili Mountains, Kazakhstan, USSR.
- Palaeostrophomena resupinata* Cooper, 1956: 704; pl. 167, figs 1–28 from Lower Benbolt Formation (L. Caradoc), Cedar Point, Hilton, Virginia, USA.
- Stropheodonta* (*Leptostrophia*) *subfilosa* Reed, 1917: 893; pl. 17, figs 9–12 from Craighead Limestone (U. Caradoc), Craighead, Girvan, Scotland (revised Williams 1962: 158; pl. 14, figs 26, 29, 30, 32).
- Palaeostrophomena superba* Cooper, 1956: 707; pl. 169, figs

13–29; pl. 184, figs 13–18 from M. Arline Formation (L. Caradoc), Friendsville, Tennessee, USA.

Palaeostrophomena subtransversa Cooper, 1956: 707; pl. 168, figs 11–13 from Arline Formation (L. Caradoc), Porterfield Quarry, Virginia, USA.

SPECIES QUESTIONABLY ASSIGNED

Palaeostrophomena? majori Spjeldnaes, 1957: 64; pl. 1, fig. 13 from Bryozoan Zone (Caradoc), Saltboden, Freierfjorden, Langesund–Gjerpen district, Norway (no brachial valve internal known).

Palaeostrophomena? rugosa Cooper, 1956: 705; pl. 176, figs 6–12 from Botetourt Formation (L. Caradoc), Lexington, Virginia, USA (rugate).

TOQUIMIA Ulrich & Cooper, 1936 Figs 59–61

- 1936 *Toquimia* Ulrich & Cooper: 626
1938 *Toquimia* Ulrich & Cooper: 183
1956 *Toquimia* Cooper: 698
1965 *Toquimia* Williams: H372
1970 *Toquimia* Ross: 63
1974 *Ishimia* Nikitin: 59

TYPE SPECIES. *Toquimia kirki* Ulrich & Cooper. Type species of *Ishimia* is *I. ishimensis* Nikitin, 1974.

DIAGNOSIS. Large flabellate pedicle valve muscle field. Bulbous cardinal process with massive central component and small lateral processes. Large pseudodeltidium, small chilidium variably developed. Like *Apatomorpha* but with platform.

REMARKS. *Toquimia* is transferred from the Taffiidae (where it has always been classified) because it possesses a trifold, not a simple cardinal process, as seen in Cooper 1956: 698; pl. 164, figs 11, 13. Ross (1970: 64; pl. 8, fig. 17) has found some bilobed structures on sectioning some specimens, but he and Cooper are not certain from this sectioned material whether *Toquimia* has a bilobed cardinal process or not. Of course if it had, then the genus would be classified as an early member of the Strophomenacea, but from the pictures of Cooper (1956: pl. 164) we believe *Toquimia* to be correctly placed within the Leptellinidae. In fact, there is some variability in the external form of the cardinal process, but no generic differences between *T. kirki* and *I. ishimensis*. We agree with Nikitin (1974: 61) in his comment that *Ishimia* is very close to *Titanambonites*, and that it would be possible to unite them within the Leptellinidae, even though his concept of the Leptellinidae differs from ours in the systematic value of the possession of a platform. The brachial valve of *Ishimia* and *Titanambonites* are virtually identical, apart from the platform in *Ishimia*. Some excellent specimens of *Toquimia*

aranaea are available to us from old collections made by Strachey in the western Himalayas (Indo-Chinese border area) in the 1840s (Figs 59–61).

SPECIES ASSIGNED

Apatomorpha altaicus Severgina, 1960: 406; pl. 0–17, figs 19–21 from Khankharin Formation (U. Llandeilo), River Ebogon, Gornoi Altai, USSR.

Strophomena aranea Salter, in Salter & Blanford 1865: 36; pl. 3, fig. 10 from Lower Ordovician beds, Damchen, Niti, NW India, and its synonym *Strophomena nubigena* Salter, in Salter & Blanford 1865: 37; pl. 3, fig. 11 from similar beds at Upper Rimkin, Niti.

Plectambonites crassus Willard, 1928: 278; pl. 3, fig. 10 from Effna Formation (L. Caradoc), Bland, Virginia (revised by Cooper, 1956: 720; pl. 181, figs 1–9 as *Titanambonites crassus* but has platform).

Ishimia humilis Nikitin, 1974: 62; pl. 6, figs 1–3 from Bestamak Formation, Yekebidaik Horizon (M. Caradoc), Sakbay, Chinghiz Mountains, Kazakhstan, USSR.

Ishimia ishimensis Nikitin, 1974: 61; pl. 5, figs 10–16 from Andryshenskaya Formation (U. Llanvirn?), Ishim River, Kazakhstan, USSR.

Toquimia kirki Ulrich & Cooper, 1936: 626; from U. Pogonip (Llanvirn), Ikes Canyon, Nevada, USA (also Cooper, 1956: 698; pl. 164, figs 4–14; pl. 195, fig. 32; Ross 1970: pl. 8, figs 16, 18).

Titanambonites magnus Nikitin, 1974: 56; pl. 5, figs 1–5 (from same locality and horizon as *I. ishimensis* and probably a synonym).

Ishimia mediasiaticia Misius, 1986: 145; pl. 9, figs 18–24; pl. 10, figs 1–23 from Tabilgat Formation (U. Llandeilo), River Tabilgat, Moldo-Too, N. Kirgiziya, USSR.

Titanambonites planus Rozman, 1964: 148; pl. 13, figs 1–7 from U. Kalychan Formation (M. Ordovician), River Kalychan, Seleniakh Mountains, NE USSR.

Ishimia radiata Nikitin, 1974: 64; pl. 6, figs 7–10 (from same locality and horizons as *I. ishimensis* and probably a synonym).

Ishimia sumsarica Rozman, 1978: 88; pl. 14, figs 9–12 from Obikalon Beds (U. Caradoc), Shakhriomon, Tian-Shan, USSR.

NOMEN NUDUM. *Ishimia? triangula* Nikitin, 1974: 59.

SPECIES QUESTIONABLY ASSIGNED

Toquimia? asiatica Borissiak, 1972: 182; pl. 49, figs 1–3 from *Catenipora* Beds (Ashgill), Abaktiigen River, Tarbagatau Mountains, E. Kazakhstan, USSR (no brachial valve interior illustrated).

Ishimia narulgensis Nikitin, 1974: 63; pl. 6, figs 4–6 from Tselinograd Horizon (Llandeilo–L. Caradoc), Narulgen,

Figs 62, 63 *Calyptoptepta diaphragma* Neuman, 1976, paratypes from Virgin Arm Tuffs (Llanvirn), east side of Virgin Arm, New World Island, Newfoundland, Canada. Fig. 62, downward and posterior views of latex cast and oblique and downward views of natural internal mould of brachial valve, the original of Neuman 1976: pl. 6, figs 8, 9, GSC 35068a, $\times 5$, $\times 4$, $\times 6$, $\times 4$; Fig. 63, external mould of brachial valve, the original of Neuman 1976: pl. 6, fig. 7, GSC 35068b, $\times 4$.

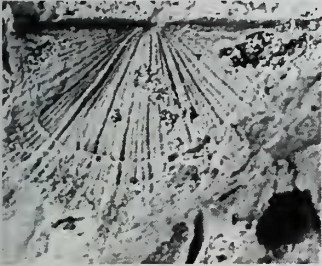
Figs 64–67 *Grorudia grorudi* Spjeldnaes, 1957, from Zone 4a β (L. Caradoc), east of Tåsen Station, Oslo, Norway. Fig. 64, natural mould and latex cast of brachial valve interior, holotype, the original of Spjeldnaes 1957: pl. 1, fig. 10, PMO 66939, $\times 8$; Fig. 65, natural mould and latex cast of brachial valve interior, figured by Spjeldnaes 1957: pl. 1, fig. 9 as *Alwynella osloensis*, PMO 66931/69931, $\times 8$; Fig. 66, latex cast of brachial valve exterior, the original of Spjeldnaes 1957: pl. 1, fig. 5 (upper), PMO 66940, $\times 8$; Fig. 67, latex cast of brachial valve interior, figured by Spjeldnaes 1957: pl. 1, fig. 5 (lower) as the holotype of *Alwynella osloensis*, PMO 66940, $\times 8$.



62a



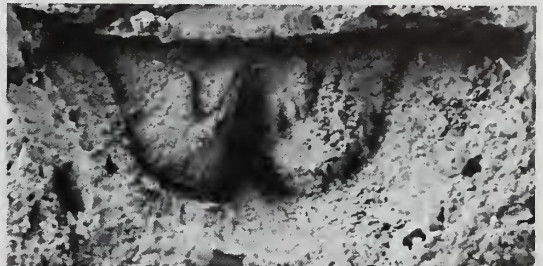
62b



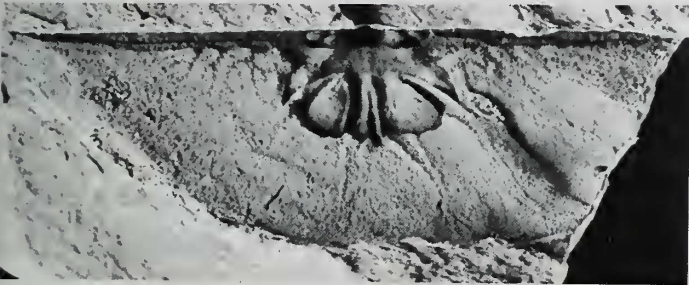
63



62c



62d



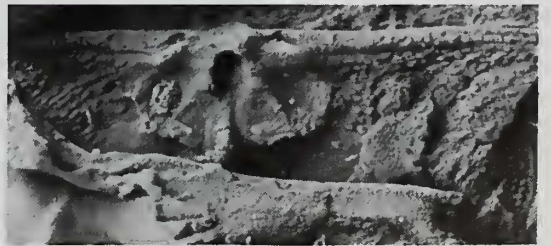
64a



64b



65a



65b



66



67

Kazakhstan, USSR (no brachial internal figured – could be *Titanambonites*).

Family GRORUDIIDAE nov.

DIAGNOSIS. Cardinal process trifold, not undercut. Bema present. Side septa present, but sometimes weakly developed. Platform variably developed.

REMARKS. We have placed *Yuanbaella* in synonymy with *Calypsolepta*. When better collections of all the forms are available then *Calypsolepta* and perhaps *Anechophragma* might properly be regarded as synonyms of *Tetraodontella* itself. *Grorudia* is revised here and now includes *Alwynella*; it is the only member of the family without a platform.

GENERA ASSIGNED. *Anechophragma* Neuman, 1977; *Calypsolepta* Neuman, 1977 (including *Yuanbaella* Fu, 1982); *Grorudia* Spjeldnaes, 1957 (including *Alwynella* Spjeldnaes, 1957); *Tetraodontella* Jaanusson, 1962.

RANGE. L. Llanvirn (*Tetraodontella* spp.) to M.–U. Caradoc (*Tetraodontella transversa*).

ANECHOPHRAGMA Neuman, 1977

1977 *Anechophragma* Neuman: 37
non 1984 *Anechophragma* Xu & Liu: 204

TYPE SPECIES. *Anechophragma rarum* Neuman, 1977.

DIAGNOSIS. Like *Calypsolepta* but with very wide teeth and no dental plates.

REMARKS. The type specimens of the aptly-named *Anechophragma rarum* have been checked by us and they have very wide teeth (see Neuman 1977: pl. 5, fig. 22) and no dental plates, in contrast to the narrow teeth with short dental plates of *Calypsolepta diaphragma* which occurs in the same bed. In addition there are a pair of very thin structures projecting anteriorly from the bema of *Anechophragma* which may be interpreted simply as an exaggerated part of the bema itself or alternatively as thin and short side septa. We are undecided whether or not the two species (and therefore the two genera) are in fact separate or really variants of each other. They provisionally remain separate here until further material is available (see also below under *Calypsolepta*).

SPECIES ASSIGNED

Anechophragma rarum Neuman, 1977: 38; pl. 5, figs 22–25 from tuffs of Llanvirn age, Virgin Arm, New World Island, Newfoundland, Canada.

CALYPTOLEPTA Neuman, 1977

Figs 62, 63

1977 *Calypsolepta* Neuman: 35
1982 *Yuanbaella* Fu: 116
1984 *Anechophragma* Xu & Liu: 204

TYPE SPECIES. *Calypsolepta diaphragma* Neuman, 1977. Type species of *Yuanbaella* is *Tetraodontella truncata* Fu, 1975.

DIAGNOSIS. Like *Tetraodontella* but with two distinct side septa in the median part of the brachial valve, no median septum. Platform present.

REMARKS. When Neuman erected *Calypsolepta* and *Anechophragma* he did not compare them with each other and also did not compare them with *Tetraodontella*, to which they are closely related. In fact the type species of the two genera are very similar (except that there are no dental plates in *Anechophragma*) and in particular include very distinctive partly united side septa in the brachial valve extending beyond the bema and a distinctive small median septum in the central region of the pedicle valve. Neuman (1977: 35) described only a 'median ridge' in *Calypsolepta*, but his photographs, including the holotype (pl. 6, figs 5, 6), clearly show that it is in fact a double septum and not a single ridge. When Fu (1982) established *Yuanbaella*, he did not compare it with *Calypsolepta* or *Anechophragma*, although he did say how it differed from *Tetraodontella*. All three nominal taxa have a very distinctive pedicle valve structure in common, with a small central median septum to either side of which are two recesses into which fitted the two side septa of the brachial valve. Certainly *Yuanbaella* should be considered as a junior synonym of *Calypsolepta*, but we have only questionably assigned *Anechophragma* in this paper because no dental plates can be seen in the sparse type material. Further investigation is needed, although original material of *Calypsolepta diaphragma* is illustrated here.

SPECIES ASSIGNED

Tetraodontella chengkouensis Xu, Rong & Liu, 1974: 149; pl. 65, figs 21–23 from Houping Formation (Llanvirn), Chengkou, N. Sichuan Province, China (also '*Anechophragma chengkouensis* sp. nov.' of Xu & Liu 1984: 205; pl. 13, figs 15–18 described on the same specimens).
Calypsolepta diaphragma Neuman, 1977: 36; pl. 6, figs 5–16 (? non figs 17, 18 which may be a leptellinid) from tuffs of Llanvirn age, Virgin Arm, Newfoundland, Canada.
Tetraodontella truncata Fu, 1975: 108; pl. 12, figs 12–18 from Xiliangsi Formation (L. Llanvirn), Dangmengou, Yuanba, Nanzheng County, S. Shaanxi Province, China.

GRORUDIA Spjeldnaes, 1957

Figs 64–67

1957 *Grorudia* Spjeldnaes: 61
1957 *Alwynella* Spjeldnaes: 85
1965 *Grorudia* Williams: H373
1965 *Alwynella* Williams: H381

TYPE SPECIES. *Grorudia grorudi* Spjeldnaes, 1957. Type species of *Alwynella* is *Alwynella osloensis* Spjeldnaes, 1957.

DIAGNOSIS. Like *Tetraodontella* and *Calypsolepta* but with no platform and side septa not extending beyond bema. Short median septum also present.

REMARKS. This genus has not been revised since its original erection by Spjeldnaes (1957), and a larger collection of toptype material illustrating the interior would be desirable. However, the original types, reillustrated here, have been examined by us. There are three brachial valve interiors from Tåsen, the common type locality of both the type species of *Grorudia* and *Alwynella*. All three show a very similar cardinal process which is not truly undercut but which has a small depression anteriorly to it in the valve floor. There is no doubt that all three specimens (which include the holotypes of *Grorudia grorudi* and *Alwynella osloensis*) belong to the same species – all have a very characteristic small median septum

with a swollen knob at the anterior end and interesting small semicircular bemas. Two of the three specimens (PMO 6931, Fig. 65 and PMO 66939, Fig. 64) have distinct side septa confined within the bema, the third (PMO 66940, Fig. 66) has side septa only faintly developed, but appears to represent a younger growth stage. There is some doubt on the nature of the hinge line; Spjeldnaes describes *Grorudia* as having a smooth hinge line (1957: 61) but *Alwynella* as possessing crenulations (1957: 86). All the specimens we have seen have smooth hinge lines apart from PMO 66931 (Fig. 65) which has some small structures on the hinge line, but these appear too irregular to be termed denticulations.

SPECIES ASSIGNED

Grorudia ? *glabrata* Spjeldnaes, 1957: 63; pl. 1, figs 4, 8, 18 from Zone 4a β -4ba (L. Caradoc), Blindern, Oslo, Norway.

Grorudia *grorudi* Spjeldnaes, 1957: 62; pl. 1, figs 7, 10, 11 from Zone 4a β (L. Caradoc), Tåsen, Oslo, Norway, and its junior synonym *Alwynella osloensis* Spjeldnaes, 1957: 86; pl. 1, figs 5, 14, ?fig 9 from the same horizon and locality.

TETRAODONTELLA Jaanusson, 1962

Fig. 68

1962 *Tetraodontella* Jaanusson: 11965 *Tetraodontella* Williams: H376TYPE SPECIES. *Tetraodontella biseptata* Jaanusson, 1962.DIAGNOSIS. Like *Calyptolepta* but with double median septum, united posteriorly and centrally. Weak platform present.

Fig. 68 *Tetraodontella biseptata* Jaanusson, 1962, from Dalby Limestone (M. Caradoc), Sweden, brachial valve interior (based on Williams 1965: fig. 240.2c), $\times 6.5$.

REMARKS. Only two brachial valve interiors of the type species have been illustrated; one (Jaanusson 1962: pl. 1, figs 4-16) has a slim central shaft to the cardinal process, whilst the other (Williams 1965: fig. 240, 2c) has a large bulbous cardinal process (Fig. 68). Thus further collection, analysis and illustration of topotype specimens is clearly desirable, since these two illustrated specimens seem so different from each other.

SPECIES ASSIGNED

Tetraodontella biseptata Jaanusson, 1962: 3; pl. 1, figs 11-18 from Dalby Limestone (M. Caradoc), Böda Hamn borehole, Öland, Sweden.

SPECIES QUESTIONABLY ASSIGNED

Tetraodontella aquiloides Fu, 1975: 109; pl. 12, fig. 19 from Xiliangsi Formation (L. Llanvirn), Liangshan, Nanzheng County, S. Shaanxi Province, China (no interiors illustrated).

Tetraodontella transversa Chen, in Fu 1982: 116; pl. 34, fig. 12 from Pagoda Limestone (M.-U. Caradoc), Liangshan,

Nanzheng County, S. Shaanxi Province, China (no interiors illustrated).

SPECIES REJECTED

Tetraodontella chengkouensis Xu, Rong & Liu, 1974: 149; pl. 65, figs 21-23 from Houping Formation (Llanvirn), Chengkou, N. Sichuan Province, China (to *Calyptolepta*).

Tetraodontella truncata Fu, 1975: 108; pl. 12, figs 12-18 from Xiliangsi Formation (L. Llanvirn), Dangmengou, Yuanba, Nanzheng County, S. Shaanxi Province, China (to *Calyptolepta*).

Family LEPTESTIIDAE Öpik, 1933 emend.

1933	Leptestiinae Öpik: 24 <i>pars</i>
1953	Leptestiidae Williams: 6 <i>pars</i>
1956	Leptestiidae Cooper: 700 <i>pars</i>
1961	Leptestiinidae Havlíček: 447
1965	Leptestiidae Williams: H372 <i>pars</i>
1965	Leptellinidae Williams: H376 <i>pars</i>
1967	Leptestiinidae Havlíček: 29 <i>pars</i>
1970	Leptestiininae Cocks: 156

DIAGNOSIS. With bema, no side septa. Trifid cardinal process not undercut.

REMARKS. We have completely changed the concept of the Leptestiidae from that of both Öpik (1933) and also Williams (1965). In fact our concept of the family closely corresponds to that of the Subfamily Leptestiininae of Havlíček (1961) and Williams (1965), with the addition of *Leptestia* itself. We do not know of any basis or justification for splitting this natural group into subfamilies. However, there are three types of bema, the first elongate (as in *Leptestia*), the second transverse (as in our new genus *Rurambonites*) and the third divided (as in *Bilobia*). Although most of the leptestiid genera can be allocated unequivocally to one of these groups, nevertheless there is some variation (especially between the second and third groups) and thus we do not divide the genera into separate subfamilies. Two genera, *Sampo* and *Rurambonites*, have denticulate hinge lines; the rest do not.

GENERA ASSIGNED. *Bilobia* Cooper, 1956; *Leangella* (*Leangella*) Öpik, 1933, including *Diambonia* Cooper & Kindle, 1936, *Tufoleptina* Havlíček, 1961 and *Leangella* (*Opikella*) Amsden, 1968; *Leangella* (*Leptestiina*) Havlíček, 1952; *Leptestia* Bekker, 1922; *Rurambonites* gen. nov.; *Sampo* Öpik, 1933.

RANGE. L. Caradoc (*Bilobia* spp.) to L. Ludlow (*Leangella segmentum*).

BILOBIA Cooper, 1956

Figs. 69-71

1956 *Bilobia* Cooper: 7591965 *Bilobia* Williams: H378TYPE SPECIES. *Bilobia hemisphaerica* Cooper, 1956.

DIAGNOSIS. Strongly convex, divided bema, small platform.

REMARKS. There is variability in the shape of the bema, for example the specimen of *Bilobia musca* illustrated by Cooper (1956: pl. 192, fig. 23) has a bema which is united for most of its length whereas the specimen illustrated here (Fig. 70) has a bema united posteriorly for half its length and divided

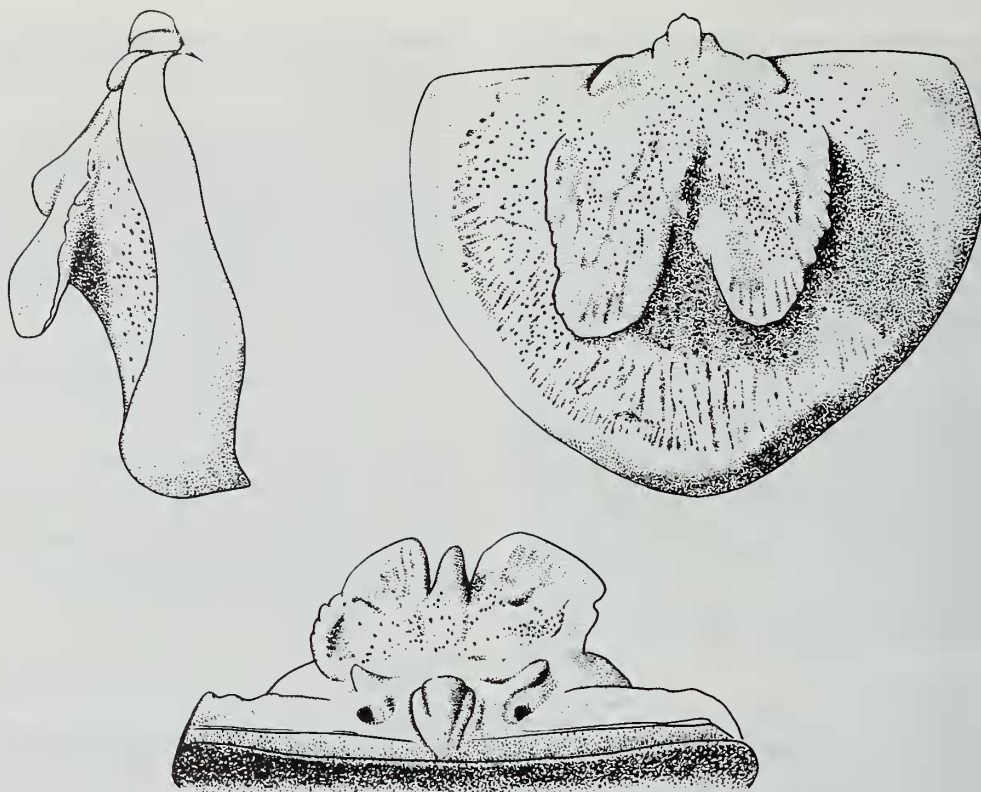


Fig. 69 *Bilobia musca* (Öpik, 1930), from Kukruse Formation (L. Caradoc), Kohtla-Järve, Estonia, USSR, interior of brachial valve showing the very elevated bema (based on BB 5202), $\times 12$.

anteriorly, which is why *musca* is assigned to *Bilobia* rather than given its own new genus.

SPECIES ASSIGNED

Leptaena etheridgei Davidson, 1883: 170; pl. 12, figs 11, 12 from Craighead Limestone (U. Caradoc), Craighead, Girvan, Scotland, and subspecies *B. etheridgei acuta* Williams, 1962: 168; pl. 16, figs 3–7 from L. Ardwell Mudstones (M. Caradoc), Ardmillan Braes, Girvan, Scotland.

Bilobia hemisphaerica Cooper, 1956: 760; pl. 192, figs 16–20; pl. 193, figs 10–36; pl. 194, figs 31–36 from Oranda Formation (L. Caradoc), Strasburg, Virginia, USA.

Bilobia huanghuaensis Chang, 1983: 477; pl. 1, fig. 22 from U. Miaopo Formation (L. Caradoc), Huanghuachang, Yichang, Hubei, China.

Sampo indentata Spjeldnaes, 1957: 69; pl. 2, figs 15–16; pl. 4, fig. 8 from 4by beds (M. Caradoc), west of Billingstad Station, Asker, Norway (revised Harper & Owen 1984: 29; pl. 3, figs 10, 12–15, 17–19, 21, 22, 24, 26, as *Leptestiina indentata*).

Leptelloidea musca Öpik, 1930: 140; pl. 8, figs 95, 97–108 from Idavere Formation (M. Caradoc), Kohtla, near Tallinn, Estonia, USSR.

Leptelloidea rosendahli Spjeldnaes, 1957: 75; pl. 2, figs 4, 5 from *Coelosphaeridium* Beds (M. Caradoc), Fangberget, Ringsaker, Norway.

Sowerbyites vesciseptus Percival, 1979: 106; fig. 7B.1–13 from Goonumbra Volcanics (L. Caradoc), Gunningbland, New South Wales, Australia.

Bilobia virginensis Cooper, 1956: 762; pl. 192, figs 1–15; pl. 195, figs 6–8 from Edinburg Formation (L. Caradoc), Strasburg, Virginia, USA.

SPECIES QUESTIONABLY ASSIGNED

Plectambonites pisum Ruedemann, 1901: 19; pl. 1, figs 8–20 from Rysedorf Conglomerate (M. Ordovician), Rysedorf, Rensselaer County, New York, USA (difficult figures, but assigned to *Bilobia* by Cooper 1956: 762).

LEANGELLA (*LEANGELLA*) Öpik, 1933 Figs 72–77

1933	<i>Leangella</i> Öpik: 42
1936	<i>Diambonia</i> Cooper & Kindle: 356
1961	<i>Tufoleptina</i> Havlíček: 447
1965	<i>Leangella</i> Williams: H378
1967	<i>Tufoleptina</i> Havlíček: 33
1968	<i>Leangella</i> (<i>Opikella</i>) Amsden: 48
1970	<i>Leangella</i> Cocks: 156

TYPE SPECIES. *Plectambonites scissa* var. *triangularis* Holtedahl, 1916, a junior subjective synonym of *Leptaena scissa* Davidson, 1871. Type species of *Diambonia* is *Plectambonites gibbosa* Winchell & Schuchert, 1892. Type species of *Tufoleptina* is *T. tufogena* Havlíček, 1961 and type species of *Opikella* is *L. (O.) dissitucostella* Amsden, 1968.

DIAGNOSIS. Bema bilobed anteriorly. Platform near valve margin.

REMARKS. The structure we term a platform near the valve margin of *Leangella* has also sometimes been termed a peripheral rim (Fig. 1, p. 79). We are certain that it is a true platform in, for example, *Leangella segmentum* (Cocks 1970: pl. 3, fig. 1); however, in many species, including the type

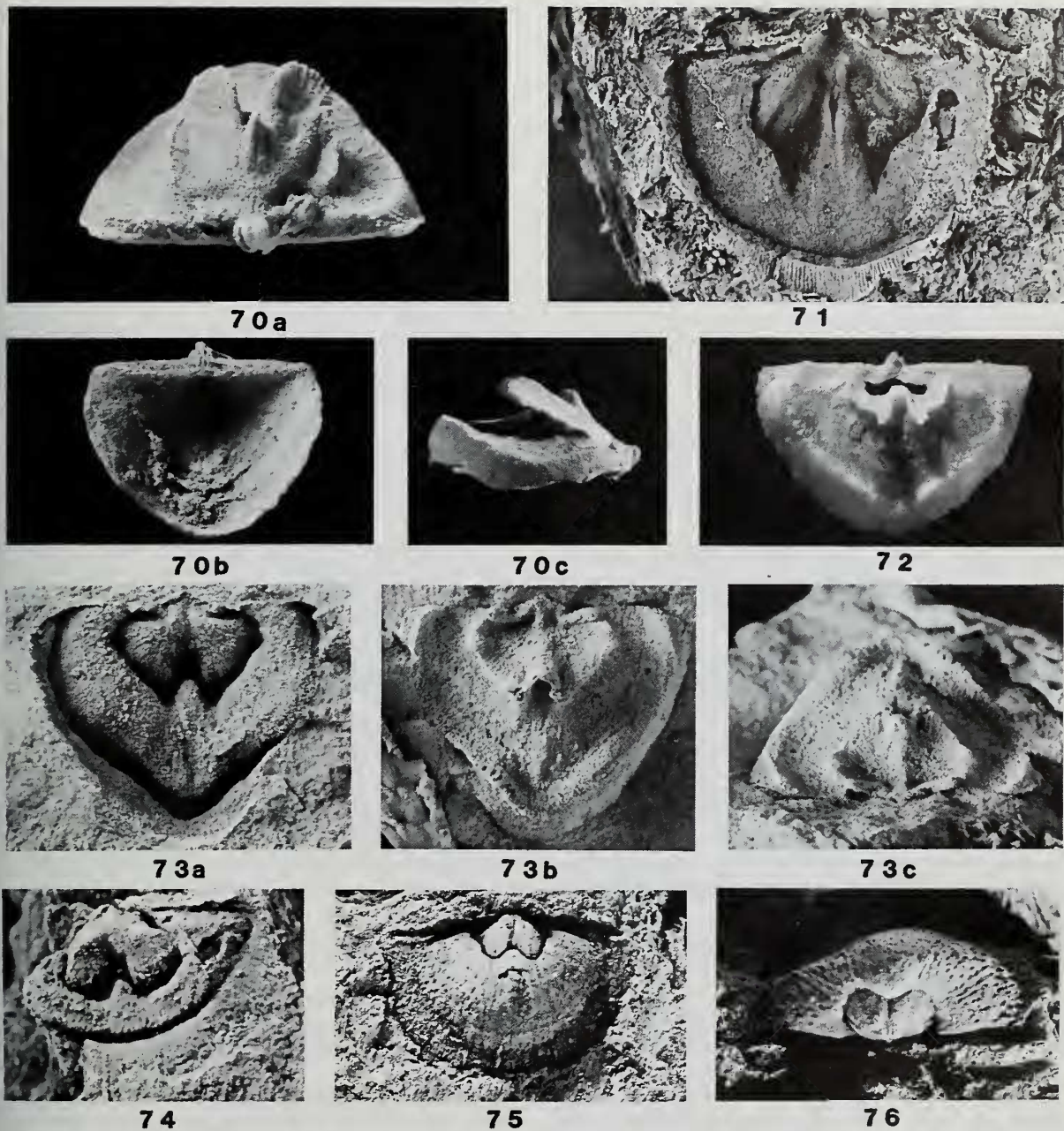


Fig. 70 *Bilobia musca* (Öpik, 1930), from Kukruse Formation (L. Caradoc), Kohtla-Järve, Estonia, USSR, posterior, exterior and lateral views of brachial valve, topotype, BB 5202, $\times 7$ (70a) and $\times 5$ (70b, c).
 Fig. 71 *Bilobia hemisphaerica* Cooper, 1956, paratype from Oranda Formation (L. Caradoc), Guilford Springs, 2.5 miles SW of Chambersburg, Pennsylvania, USA, internal mould of brachial valve, the original of Cooper 1956: pl. 193, figs 34, 35, USNM 111087c, $\times 5$.
 Fig. 72 *Leangella (Leangella) gibbosa* (Winchell & Schuchert, 1892), from Stewartville Formation (L. Ashgill), between Stewartville and Chatville, Minnesota, USA, silicified interior of brachial valve, BC 7272, $\times 5$.
 Fig. 73 *Leangella (Leangella) scissa* (Davidson, 1871), topotype from U. Haverford Mudstone Formation (L. Llandovery), Gasworks, Haverfordwest, Dyfed, Wales, natural internal mould and downwards and posterior views of latex cast of brachial valve, BB 32167, $\times 6$.
 Figs 74–76 *Leangella (Leangella) tufogena* (Havlíček, 1961), topotypes from Liteň Formation (U. Wenlock), Hliník, Svätý Jan Pod Skalou, Bohemia, Czechoslovakia. Fig. 74, natural internal mould of brachial valve, BB 71535, $\times 8$; Fig. 75, natural internal mould of pedicle valve, BB 71530, $\times 6$; Fig. 76, natural internal mould of pedicle valve viewed obliquely from the posterior, BB 71536, $\times 8$.

species, this platform is not developed so strongly and its function is less certain. There is some variation in the median septum in the brachial valve – this is usually a double septum, sometimes a single septum and in some specimens no septum

at all can be seen. Likewise the median septum in the pedicle valve is also variably developed; in some populations (e.g. that figured in Mitchell 1977: pl. 15) the septum is present in some specimens and absent in others, and for this reason we

do not separately recognize *Diambonia* as a valid genus. In addition, the brachial valves of '*Leangella*' and '*Diambonia*' are identical. Havlíček erected *Tufoleptina* on the basis of the extra presence of a submarginal ridge in the pedicle valve, but Cocks (1970: 157) has demonstrated the variable occurrence of this ridge in several *Leangella* populations and so we do not accept *Tufoleptina* as valid. *Opikella* differs from *Leangella* only in lacking the finer radial ornament; however, it still possesses normal costellae and we do not think the differences merit more than specific separation; we do not use the term for a separate subgenus or genus.

SPECIES ASSIGNED

Leangella anaclyta Havlíček, 1981: 21; pl. 7, figs 19–27 from M.–U. Caradoc, La Grange-du-Pin, Montagne Noire, France (revised Villas 1985: 85; pl. 18, figs 13–14; pl. 19, figs 1–15).

Diambonia anatoli Spjeldnaes, 1957: 80; pl. 2, figs 6–8 from Zone 4ba (M. Caradoc), Nesøya, Oslo, Norway.

Leangella auritus Su, 1980: 271; pl. 116, figs 11–14 from Huanghuagou Formation (M. Llandovery), east side of Luohe River, Aihui County, Heilongjiang Province, NE China.

Plectambonites quinquecostata var. *cylindrica* (= *Leangella cylindrica*) Reed, 1917: 878; pl. 14, figs 11, 14–17 non figs 12, 13 from Shalloch Formation (L. Ashgill), Shalloch Mill, Girvan, Scotland.

Leangella discuneata Lamont, 1935: 315; pl. 7, figs 17–19 from Auld Thorns Conglomerate (L. Ashgill), Auld Thorns, Girvan, Scotland (revised Mitchell 1977: 78; pl. 15, figs 10–25).

Leangella (Opikella) dissitocostella Amsden, 1968: 48; pl. 5, figs 1a–q; pl. 16, figs 1a–e; pl. 19, figs 2a–b from St Clair Limestone (L. Wenlock), Batesville, Arkansas, USA.

Plectambonites gibbosa Winchell & Schuchert, 1892: 288 from Caradoc beds, Mantorville, Old Concord, Tennessee, USA.

Leangella hamari Spjeldnaes, 1957: 81; pl. 2, figs 1–3 from Cyclocrinus Shale (M. Caradoc), Furuberget, Hamar-Nes district, Norway.

Leangella ino Öpik, 1953: 13; pl. 2, figs 5–11; pl. 3, figs 12–15 from the Illaenus Band (U. Llandovery), Heathcote, Victoria, Australia.

Leptaena scissa Davidson, 1871: 325 pars; pl. 47, figs 21–23 non figs 24, 25 from U. Haverford Mudstone Formation (L. Llandovery), Haverfordwest, Dyfed, Wales, a senior subjective synonym of *Plectambonites segmentum* var. *woodlandensis* Reed, 1917: 881; pl. 14, figs 36–41 from Woodland Formation (L. Llandovery), Woodland Point, Girvan, Scotland, and *Plectambonites scissa* var. *triangularis* Holtedahl, 1916: 84; pl. 15, figs 5–6 from Solvik Formation (L. Llandovery), Asker, Norway (all revised Cocks 1970: 158; pl. 1, figs 11–14; pl. 2, figs 1–14; pl. 3, figs 2–14; pl. 4, figs 1–4 and Temple 1987: 55; pl. 5, figs 1–8).

Leptaena segmentum Lindström, 1861: 374 from Mulde Beds (U. Wenlock), Djupvik, Gotland, Sweden (revised Cocks 1970: 162; pl. 3, fig. 1; pl. 4, figs 7–12).

Leptelloidea septata Cooper, in Schuchert & Cooper 1930: 272; pl. 1, figs 9–13 from U. Ashgill Beds, Grande Coupe, Percé, Quebec, Canada.

Leptelloidea sholeshookensis Jones, 1928: 488; pl. 25, fig. 19 from Slade and Redhill Mudstones (M. Ashgill), Lower Cresswell, Dyfed, Wales.

Plectambonites tennesseensis Foerste, 1903: 708 from Waldron Shale (Wenlock), Clifton, Tennessee, USA.

Tufoleptina tufogena Havlíček, 1961: 449; pl. 1, figs 1–6 from U. Liten Shale (U. Wenlock), Svaty Jan pod Skalou, Bohemia, Czechoslovakia (revised Havlíček 1967: 33; pl. 1, figs 1–7).

SPECIES QUESTIONABLY ASSIGNED

Sowerbyella transversalis brevis Northrop, 1939: 176; pl. 15, figs 11–14 from Clemville Formation (L. Wenlock), Clemville, Gaspé, Quebec, Canada (no interiors known, but by its shape almost certainly a *Leangella*).

Leangella hubeiensis Chang, 1983: 478; pl. 1, figs 27–31 from Miaopo Formation (U. Llandeilo–L. Caradoc), Huanghuachang, Yichang County, Hubei Province, China (no brachial valve known).

Leptelloidea (Leangella?) lamellata Reed, 1936: 44; pl. 4, figs 22–23 from Naunkangyi Formation (L. Caradoc), hill behind Taunggyi, Southern Shan States, Burma (no brachial valve interior figured, but pedicle valve interior looks more like a sowerbyellid).

Diambonia ? leifi Spjeldnaes, 1957: 79; pl. 2, figs 9–11 from *Mastopora* Zone (Caradoc), Stranda, Langesund-Gjerpen district, Norway (interior poorly figured).

Orthis quinquecostata McCoy, 1846: 33; pl. 3, fig. 8 from U. Llandovery rocks of Coolin or Kilbride, Co. Galway, Ireland (no interiors figured; discussed Cocks, 1978: 95).

Leangella yichangensis Chang, 1983: 478; pl. 1, figs 32–34 from Miaopo Formation (U. Llandeilo–L. Caradoc), Huanghuachang, Yichang County, Hubei Province, China (no brachial interior known).

SPECIES REJECTED

Leangella magna Ushatinskaya, in Misius & Ushatinskaya 1977: 115; pl. 27, figs 1, 2 from Saribypakskaya bed (M. Llandovery), Jhelesken Hill, Kazakhstan, USSR (genus uncertain, brachial valve lacks platform).

Diambonia miaopensis Chang, 1983: 477; pl. 1, figs 12, 17 from Miaopo Formation (U. Llandeilo–L. Caradoc), Huanghuachang, Yichang County, Hubei, China (genus uncertain).

LEANGELLA (LEPTESTIINA) Havlíček, 1952

1952 *Benignites (Leptestiina)* Havlíček: 412

1965 *Leptestiina* Williams: H378 pars (non *Dulankarella*)

TYPE SPECIES. *Benignites (Leptestiina) prantli* Havlíček, 1952.

DIAGNOSIS. Like *Leangella (Leangella)* except that the 'platform' is made up anteriorly of discrete septules which are not merged to form a typical continuous platform.

REMARKS. From the type species of *Leptestiina* (e.g. Havlíček 1967: pl. 2, fig. 18) it is clear that a typical platform is absent. However, the row of discontinuous septules where a platform might be is clear indication of the very close relationship between *Leangella* and *Leptestiina*. This is further reinforced by the populations illustrated by Melou (1971: pls 1 and 2) in which a true platform is weakly developed laterally, but not anteriorly, where only septules are found; and the same is true of the population figured by Sheehan (1973: pl. 1).

SPECIES ASSIGNED

Leptestiina aonensis Melou, 1971: 95; pl. 1, figs 1–6; pl. 2, figs 1–3 from Rosan Tuffs (L.–M. Ashgill), Ster ar Poul Men, Brittany, France (transitional to *Leangella (Leangella)*).

Leptelloidea derfelensis Jones, 1928: 479; pl. 25, figs 3–7

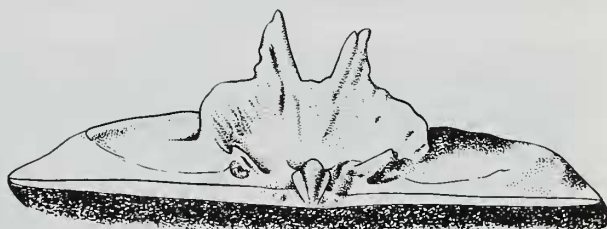


Fig. 77 *Leangella (Leangella) gibbosa* (Winchell & Schuchert, 1892), from Stewartville Formation (L. Ashgill), between Stewartville and Chatville, Minnesota, USA, lateral downward, anterior and posterior views of a brachial valve interior, based on BC 7272, $\times 9$.

(revised Melou 1971: 99; pl. 2, figs 4–9) from Derfel Limestone (L. Caradoc), Derfel Gorge, Wales.

Leptestiina meloui Havlíček, 1981: 20; pl. 7, figs 1–10 from M.–U. Caradoc rocks, Gabian, Montagne Noire, France.

Sampo oepiki Whittington, 1938: 255; pl. 10, figs 15–16; pl. 11, fig. 10 from Longvillian beds (M. Caradoc), Bryngwyn Hill, Llanfyllin, Powys, Wales (revised Williams, 1963: 428; pl. 10, figs 15, 16, 19–21).

Benignites (Leptestiina) prantli Havlíček, 1952: 412; text-fig. 1 from Králův Dvůr Shales (M. Ashgill), Králův Dvůr, Bohemia, Czechoslovakia (revised Havlíček 1967: 30; pl. 2, figs 16, 18).

Leptestiina sp. of Hurst 1979: 276; figs 399, 403, 407, 408 from Acton Scott Formation (U. Caradoc), Acton Scott, Shropshire, England.

SPECIES QUESTIONABLY ASSIGNED

Leptestiina longxianensis Fu, 1982: 117; pl. 34, figs 13–16 from U. Pingliang Formation (L. Caradoc), Shiguancun, Longxian County, Shaanxi Province, China (no adequate interior known for generic assignment).

LEPTESTIA Bekker, 1922
Figs 78, 79

- 1922 *Leptestia* Bekker: 362
- 1930 *Leptestia* Öpik: 123
- 1965 *Leptestia* Williams: H373

TYPE SPECIES. *Leptestia musculosa* Bekker, 1922.

DIAGNOSIS. With elongate bema. With platform.

REMARKS. This is the only genus within this family which has an elongate bema (apart from the denticulate *Sampo*) and is therefore easy to recognize.

SPECIES ASSIGNED

Strophomena jukesii Davidson, 1869: 296; pl. 37, figs 23–26 from beds of Caradoc age, Grangegeeth, Co. Meath, Ireland.

Leptestia musculosa Bekker, 1922: 363; text-figs 1–4 from L.–M. Kuckruse Formation (L. Caradoc), Kohtla-Järve, near Tallinn, Estonia, USSR.

SPECIES QUESTIONABLY ASSIGNED

Leptestia cita Rukavishnikova, 1956: 130; pl. 2, figs 4–7 from Kopalinsky Horizon (Llanvirn), Kyandysai, Chu-Ili Mountains, Kazakhstan, USSR (interiors poorly known).

Leptestia diaphanes Öpik, 1930: 130; pl. 7, fig. 80 from L.–M. Kuckers Formation (L. Caradoc), Kohtla, near Tallinn, Estonia, USSR (only pedicle valve figured – may be synonym of *L. musculosa*).

Leptestia sp. of Bekker 1922: 364; text-fig. 5 from Rakvere Formation (Caradoc–Ashgill), Rakvere, Estonia, USSR (only pedicle valve known).

Leptestia sp. of Xu & Liu 1984: 204; pl. 14, figs 12–14 from U. Meitan Formation (U. Arenig), Tongzi County, N. Guizhou, China (no platform visible).

SPECIES REJECTED

Leptestia (Leptoptilum) bekkeri Öpik, 1930: 131; pl. 8, fig. 81 from U. Kuckruse Formation (L. Caradoc), Kohtla, near Tallinn, Estonia, USSR (see *Leptoptilum*).

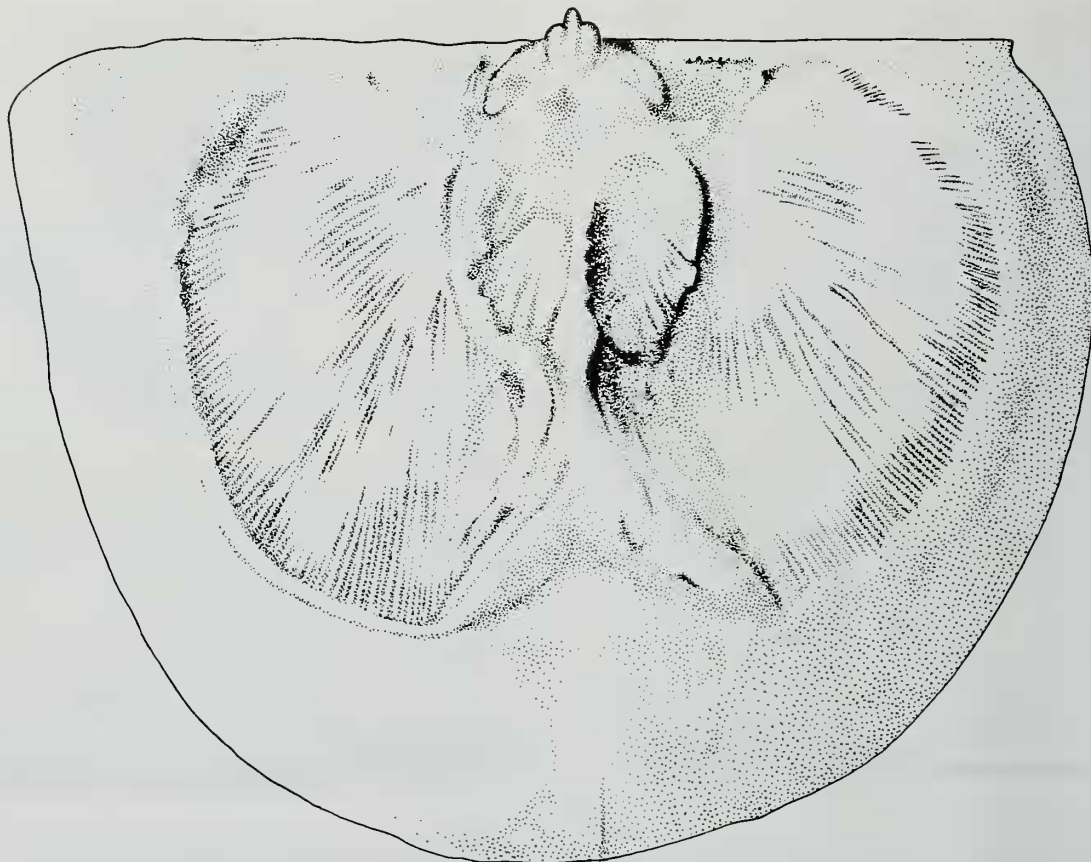


Fig. 78 *Leptestia muscolosa* Bekker, 1922, from Kukruse Formation (L. Caradoc), Kohtla-Järve, Estonia, USSR, brachial valve interior, based on BB 5189, $\times 6$.

RURAMBONITES gen. nov.

Figs 80–84

TYPE SPECIES. *Plectambonites ruralis* Reed, 1917.

DIAGNOSIS. Bema transverse and not bilobed, in contrast to the bilobed elongate bema of *Sampo*. Denticulate hinge line.

REMARKS. Öpik (1933) and others have placed *ruralis* within *Sampo*. However, we feel that the shapes of the bemas in the two genera are so different that generic separation is appropriate. We illustrate here the lectotype and additional topotype specimens (Figs 80–84). The denticles are on the pedicle valve and the pits on the brachial valve, as in *Sowerbyella* (*Eochonetes*).

SPECIES ASSIGNED

Sampo hiiuensis Öpik, 1933: 36 pars; pl. 8, fig. 5 only from F₁ Beds (U. Caradoc–L. Ashgill), Korgessaare, Hiiumaa, Estonia, USSR.

Sampo molodovensis Tsegelniuk, 1976: 60; pl. 8, figs 4–9 from Subochskaya Formation (U. Ordovician), Komarov, Podolia, Ukraine, USSR.

Plectambonites ruralis Reed, 1917: 879; pl. 14, figs 25–33 from Upper Drummuck Group (U. Ashgill), Starfish Bed, Girvan, Scotland.

SAMPO Öpik, 1933

1933 *Sampo* Öpik: 35
1965 *Sampo* Williams: H378

TYPE SPECIES. *Sampo hiiuensis* Öpik, 1933.

DIAGNOSIS. Bema elongate and bilobed. Like *Bilobia* but with denticulate hinge line.

REMARKS. In both brachial valves illustrated by Öpik (1933: pl. 7, fig. 3 and pl. 8, fig. 4) the anterior end of the bema finishes irregularly, with two main calcite platforms and additional straggly septules. It is difficult both to describe these structures unambiguously and also to assess properly their systematic significance. New collections of topotype *Sampo hiiuensis* are needed to assess properly the true variation of the bema. The disposition of the denticles is the same as in *Rurambonites*.

SPECIES ASSIGNED

Sampo hiiuensis Öpik, 1933 pars: 36; pl. 6, figs 4, 5; pl. 7, figs 1–3; pl. 8, fig. 4, non fig. 5 from Nabala Beds (U. Caradoc–L. Ashgill), Moe, Estonia, USSR.

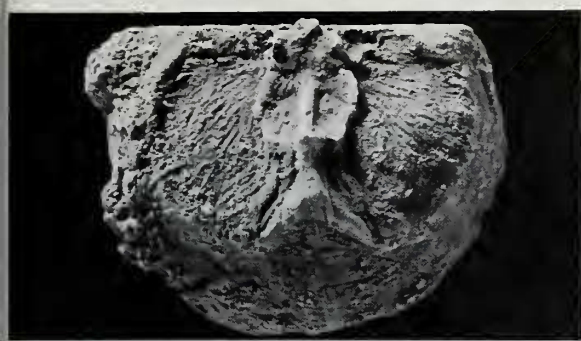
SPECIES QUESTIONABLY ASSIGNED

Sampo hiiuensis var. *mucronata* Öpik, 1933: 39; fig. 2E from Rakvere Formation (U. Caradoc), Pühalepa, Hiiumaa, Estonia, USSR (no interiors known).

Sampo hiiuensis var. *nasuta* Öpik, 1933: 39; pl. 8, fig. 3 from Vormsi Formation (L. Ashgill), Korgessaare, Estonia, USSR (only exterior known).

SPECIES REJECTED

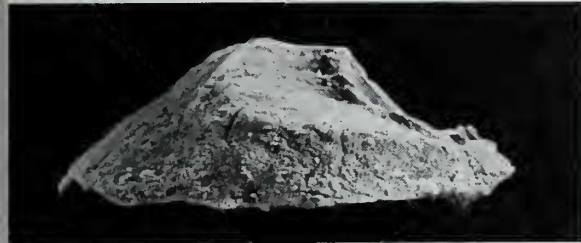
Sampo indenata Spjeldnaes, 1957: 69; pl. 2, figs 15–16; pl. 4, fig. 8 from 4by beds (M. Caradoc), west of Billingstad, Asker, Norway (to *Bilobia*).



79a



79b



79c



80



81a



81b



81c



82a



82b



81d



83a



83b



83c

Fig. 79 *Leptestia musculososa* Bekker, 1922, topotype from Kukruse Formation (L. Caradoc), Kohtla-Järve, Estonia, USSR, downward, posterior and lateral views of brachial valve, BB 5189, $\times 3$.

Figs 80–83 *Rurambonites ruralis* (Reed, 1917) gen. nov., topotypes from Starfish Bed, South Threave Formation (Ashgill: U. Rawtheyan), 650 m ENE of South Threave Farmhouse, Girvan, Strathclyde, Scotland. Fig. 80, natural internal mould of pedicle valve, BC 7202, $\times 3.5$; Fig. 81, natural internal mould and three views of a latex cast of a brachial valve, BC 7201, $\times 4$; Fig. 82, natural internal mould and latex cast of a brachial valve interior, BC 7204, $\times 4$; Fig. 83, latex cast, natural internal mould and posterior view of latex cast of a brachial valve interior, BC 7204, $\times 4$.

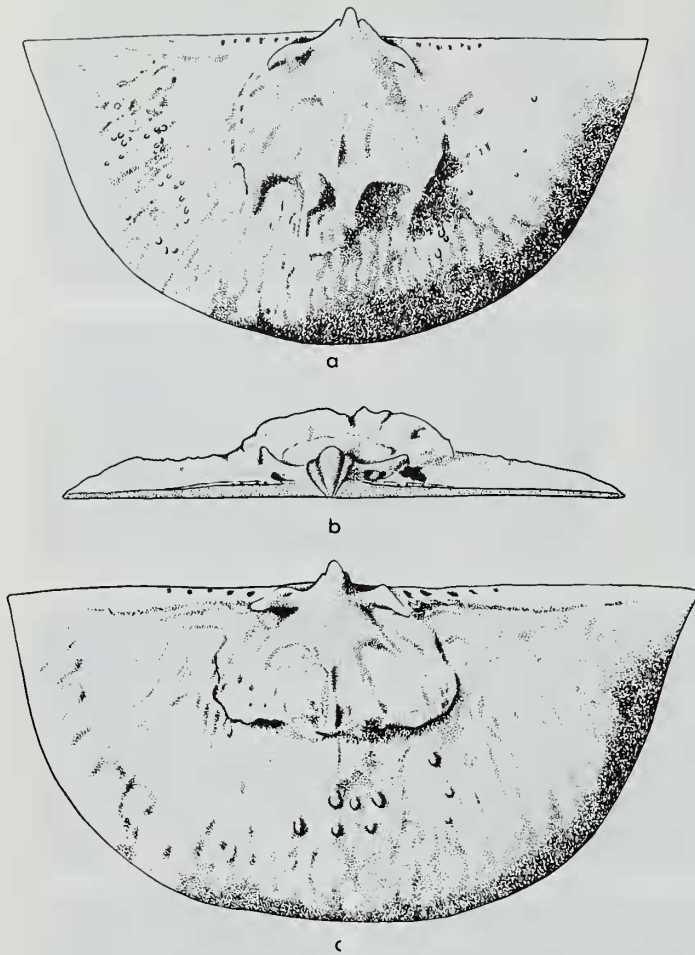


Fig. 84 *Rurambonites ruralis* (Reed, 1917) gen. nov., from Starfish Bed, South Threave Formation (Ashgill: U. Rawtheyan), Girvan, Strathclyde, Scotland, showing the bema variation in the interiors of two brachial valves (a, b after BC 7204, c after BC 7200), $\times 5$.

Sampo oepiki Whittington, 1938: 255; pl. 10, figs 15, 16; pl. 11, fig. 10 from beds of Longvillian (M. Caradoc) age, Bryngwyn Hill, Llanfyllin, Powys, Wales (to *Leptestiina*).

Family XENAMBONITIDAE Cooper, 1956

- 1956 Xenambonitinae Cooper: 813
 1965 Xenambonitinae Williams: H381
 1965 Aegiromeninae Williams: H381 *pars*
 1967 Sowerbyellidae Havlíček: 37 *pars*

DIAGNOSIS. Cardinal process undercut. With variably developed bema. No side septa.

REMARKS. Cooper's subfamily is elevated here to familial level to differentiate the group from the Sowerbyellidae, which possess side septa. The Xenambonitidae is divided into two subfamilies based on the elevated bema of the Xenambonitinae as opposed to the weak bema of the Aegiromeninae, which sometimes consists only of disconnected septules, and the presence or absence of a platform.

SUBFAMILIES ASSIGNED. Xenambonitinae Cooper, 1956; Aegiromeninae Havlíček, 1964.

RANGE. Llandeilo–Pridoli.

Subfamily XENAMBONITINAE Cooper, 1956

- 1956 Xenambonitinae Cooper: 813
 1965 Xenambonitinae Williams: H381

DIAGNOSIS. Like Aegiromeninae, but with platform. Bema elevated.

REMARKS. At first glance, xenambonitines are apparently rather different from aegiromenines in possessing a strong platform (absent in aegiromenines) and an elevated bema, rather than the weak and never elevated bema seen in aegiromenines. However, we put both within the same family because of the presence in both groups of an undercut cardinal process and a bema and because of the absence of side septa.

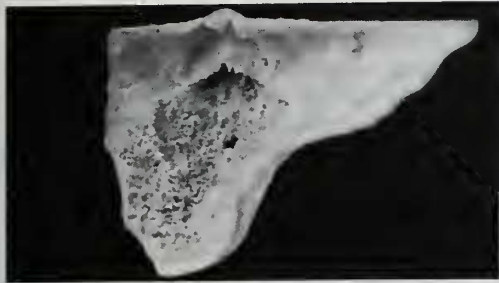
GENUS ASSIGNED. *Xenambonites* Cooper, 1956.

RANGE. Llandeilo–Caradoc.

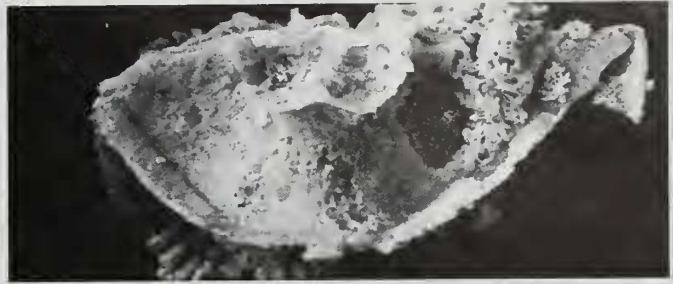
XENAMBONITES Cooper, 1956 Figs 85, 86

- 1956 *Xenambonites* Cooper: 813
 1965 *Xenambonites* Williams: H381

TYPE SPECIES. *Xenambonites undosus* Cooper, 1956.



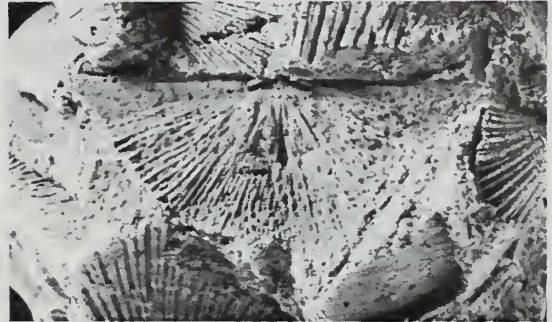
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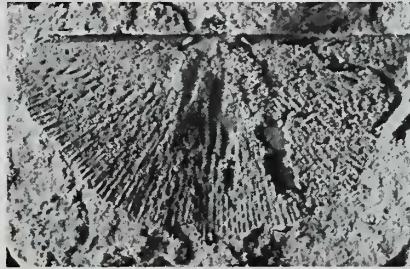
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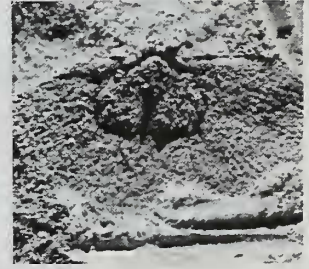
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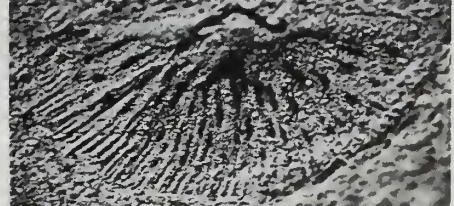
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Figs 85, 86 *Xenambonites undosus* Cooper, 1956, topotypes from Pratt Ferry Formation (Llandeilo), SE of Pratt Ferry, Blocton, Alabama, USA. Fig. 85, interior and exterior views of a silicified pedicle valve, BC 10293, $\times 12$; Fig. 86, interior of a silicified brachial valve, BC 10292, $\times 9$.

Figs 87–89 *Aegiria (Aegiria) aquila aquila* (Barrande, 1848), from Zahorany Formation (M. Caradoc), Bohemia, Czechoslovakia. Fig. 87, natural internal mould of brachial valve from Palmovka, Praha-Libeň, BC 7212, $\times 4$; Fig. 88, natural internal mould of pedicle valve from Beroun, BB 13658, $\times 5$; Fig. 89, natural internal mould of brachial valve from Sporilov, Prague, BB 33341, $\times 5$.

Fig. 90 *Aegiria (Aegiria) aquila praecursor* Havlíček, 1952, from Letná Formation (L. Caradoc), Blyskava Hill, near Chrutenice, Czechoslovakia, natural internal mould of brachial valve, BC 6831, $\times 6$.

Fig. 91 *Aegiria (Aegiria) garthensis* (Jones, 1928), topotype from Lower Llandovery beds, north of Garth, Powys, Wales, natural internal mould of brachial valve, GSM 50418, $\times 7$.

Figs 92, 93 *Chonetoidea papillosa* (Reed, 1905), from Slade and Redhill Mudstone Formation (M. Ashgill), Upper Slade, near Haverfordwest, Dyfed, Wales. Fig. 92, natural internal moulds of conjoined valves, SMA 11313, $\times 4$; Fig. 93, lectotype (selected Cocks 1970: 194), the original of Reed 1905: pl. 23, fig. 13, natural internal mould of a brachial valve, SMA 11311, $\times 10$.

DIAGNOSIS. As for family. With ventral fold and dorsal sulcus. Geniculate anteriorly towards pedicle valve.

REMARKS. *Xenambonites* is a very distinctive plectambonitacean and is given a subfamily of its own here, although we believe that the geniculation by itself is a generic rather than a familial character.

SPECIES ASSIGNED

Xenambonites revelatus Williams, 1962: 191; pl. 18, figs 21–23 from Balclatchie Conglomerate (L. Caradoc), Penwhapple Burn, Girvan, Scotland.

Xenambonites cf. *X. revelatus* of Ross & Dutro 1966: 16; pl. 2, figs 21–26 from beds of Caradoc age, Hard Luck Creek, Alaska, USA.

Xenambonites undosus Cooper, 1956: 815; pl. 195, figs 17–31; pl. 268, figs 25–38 from Pratt Ferry Formation (Llandeilo), Pratt Ferry, Alabama, USA.

Subfamily AEGIROMENINAE Havlíček, 1961

1961 Aegiromeninae Havlíček: 450
1965 Aegiromeninae Williams: H381
1967 Aegiromeninae Havlíček: 37

DIAGNOSIS. Like Xenambonitinae, but without platform. Variably developed bema, but never elevated.

REMARKS. The lack of platform differentiates this subfamily from the Xenambonitinae and the Hesperomenidae, to which the Aegiromeninae is, nevertheless, closely related. Although the absence of a bema would generally make us assign some specimens or populations of *Chonetoidea* and *Jonesea* to another family such as the Hesperomenidae, there is no doubt that the occasional loss of the bema is a secondary characteristic in the family and for this reason these forms are classified unhesitatingly within the Aegiromeninae. Even though *Aegiromena* is here considered a junior synonym of *Aegiria*, the subfamily name Aegiromeninae still stands.

GENERA ASSIGNED. *Aegiria* (*Aegiria*) Öpik, 1933, including *Aegiromena* Havlíček, 1961; *Aegiria* (*Aegironetes*) Havlíček, 1967; *Aegiria* (*Epelidoaegiria*) Strusz, 1982; *Chonetoidea* Jones, 1928, including *Sentolunia* Havlíček, 1967 and *Sericoidea* Lindström, 1953; *Jonesea* gen. nov.; *Mezounia* Havlíček, 1967.

RANGE. Llandeilo (*Aegironetes minuta*) to Pridoli (*Jonesea mariaformis*).

AEGIRIA (AEGIRIA) Öpik, 1933
Figs 87–91, 94

1933 *Aegiria* Öpik: 55
1961 *Aegiromena* Havlíček: 450
1965 *Aegiria* Williams: H381
1967 *Aegiromena* Havlíček: 39
1970 *Aegiria* Cocks: 195

TYPE SPECIES. *Aegiria norvegica* Öpik, 1933. The type species of *Aegiromena* is *Leptaena aquila* Barrande, 1848.

DIAGNOSIS Differs from *Mezounia* in the transverse bema, which is not bilobed anteriorly. Bema always present.

DISCUSSION. Now that the distinctive species centering around '*Aegiria*' *grayi* are now distinguished as a separate genus, *Jonesea* gen. nov. herein (p. 127), it is very clear that the type species of *Aegiria*, *A. norvegica*, cannot usefully be distinguished generically from *Aegiromena*, and so the two genera are placed in synonymy here. Havlíček (e.g. 1967: 39) separated the two genera on the relative strengths of what we term the bema, but in our opinion there is continuous variation in bema strength, both between species and even in the same population (e.g. *A. descendens* figured by Havlíček 1967: pl. 4) and we cannot separate them generically (see also Rong & Yang 1981: 171).

SPECIES ASSIGNED

Leptaena aquila Barrande, 1848: 228; pl. 22, figs 15, 16 from Zahoraný Formation (M. Caradoc), Praskolesy, Bohemia, Czechoslovakia (revised Havlíček 1967: 39; pl. 3, figs 1–14) and subspecies *Aegiria aquila praecursor* Havlíček, 1952: 401; pl. 1, figs 3, 4, 8 from Letná Formation (L. Caradoc), Chrštenice, Czechoslovakia (revised Havlíček 1967: 42; pl. 4, figs 1–6).

Aegiromena convexa Chang, 1981: 562; pl. 1, fig 28 from Kuanyinchiao Bed, U. Wufeng Formation (U. Ashgill), Huanghuachang, Yichang, W. Hubei Province, China (revised Rong 1984: 148; pl. 11, figs 1–9).

Aegiromena corolla Havlíček & Branisa, 1980: pl. 2, figs 1–6 from Llanvirm Sandstone, Tuctapari, Bolivia.

Aegiria descendens Havlíček, 1952: 402; pl. 2, figs 1–9 from Bohdalec Formation (U. Caradoc), Velká Chuchle, Czechoslovakia (revised Havlíček 1967: 43; pl. 4, figs 7–16).

Chonetoidea garthensis Jones, 1928: 500; pl. 25, figs 25, 26 from Lower Llandovery beds, north of Garth, Dyfed, Wales (revised Cocks 1970: 195; pl. 17, figs 4–7 and Temple 1987: 70; pl. 5, figs 16–21).

Aegiria grayi [*non A. grayi* (Davidson)] Rong, Xu & Yang, 1974: 203; pl. 95, figs 30–31 from U. Xiushan Formation (U. Llandovery), Leijiatun, Shiqian County, NE Guizhou, China (a new species also figured Yang & Rong 1982: 423; pl. 1, figs 17–23 from the same locality).

Aegiromena guichenensis Melou, 1973: 259; pl. 36, fig. 7 from ? Llandeilo schists, Traveusot, Brittany, France.

Aegiromena ? mariana Drot, in Chauvel *et al.* 1970: 618; pl. 13, figs 14, 14a (revised Melou 1973: 254; pl. 33, figs 1–5; pl. 34, figs 1–8; pl. 35, figs 1–9; pl. 36, figs 1–3) from Bed 13 (Llandeilo–Caradoc), El Centenillo, Sierra Morena, Spain (also refigured Villas 1985: 91; pl. 20, figs 11–18).

Orthis (Dalmanella) meneghiniana Vinassa, 1927: 461; pl. 2, figs 28–35 (revised Havlíček 1981: 22, pl. 7, figs 11–18) from Portixeddu Formation (U. Caradoc), Gùtturu màndara o punta Giovasanna, Sardinia, Italy.

Aegironetes minuta Xu, Rong & Liu, 1974: 152; pl. 66, figs 9–12 from Shihtzipu Formation (Llandeilo), Zunyi, N. Guizhou Province, China.

Aegiria norvegica Öpik, 1933: 55; pl. 10, figs 1–5; pl. 11, figs 3–5 from the Solvik Formation (L. Llandovery), Leangen, Asker, Norway.

Aegiria shiqianensis Yang & Rong, 1982: 423; pl. 1, figs 7–16 from U. Xiushan Formation (U. Llandovery), Leijiatun, Shiqian County, NE Guizhou, China.

SPECIES QUESTIONABLY ASSIGNED

Aegiria norilskensis Lopushinskaya, 1976: 38; pl. 3, figs 9–14 from *Dalmanella neocrassa* beds (M. Llandovery), S. Pyasinskaya, N. Siberia, USSR (no interiors figured).

SPECIES REJECTED

Aegiromena durbenensis Nikitin, in Nikitin et al. 1980: 52; pl. 13, figs 16–22 from Durben Formation (U. Ashgill), Durben, Chu-Ili Mountains, Kazakhstan, USSR (to *Jonesea* gen. nov.).

Aegiromena incerta Wan, 1982: 41; pl. 11, figs 19, 20 from Shihniulan Formation (U. Llandovery), Guanyinqiao, Qijiang County, Sichuan Province, SW China (to *Jonesea* gen. nov.).

Aegiria mariaformis Lenz, 1977a: 67; pl. 8, figs 6–9, 12–21 from L. Road River Formation (Pridoli), Royal Creek, Yukon, Canada (to *Jonesea* gen. nov.).

Aegiromena praeultima Mikuláš, 1983: 5; pl. 1, figs 1–9 from Podolí iron ore horizon of Králův Dvůr Formation (L.–M. Ashgill), Vlnitá ulice, Praha-Braník, Czechoslovakia (to *Jonesea* gen. nov.).

Aegiromena ultima Marek & Havlíček, 1967: 281; pl. 3, figs 9–12 from Kosov Formation (U. Ashgill), Bechovice, Czechoslovakia (to *Jonesea* gen. nov.).

Aegiromena urbana Havlíček, 1967: 44; pl. 4, figs 24–26 from Králův Dvůr Formation (L.–M. Ashgill), Praha-Podolí, Czechoslovakia (to *Jonesea* gen. nov.).

Aegiria thomasi Talent, 1965: 24; pl. 6, figs 1, 3, 5–7 from Dargile Formation (Ludlow), Heathcote, Victoria, Australia (to *Jonesea* gen. nov.).

Aegiromena yanheensis Rong & Yang, 1981: 171; pl. 2, figs 17–25 from Leijaitung Formation (U. Llandovery), Ganxi, Yanhe County, NE Guizhou Province, China (to *Jonesea* gen. nov.).

AEGIRIA (AEGIRONETES) Havlíček, 1967

1967 *Aegironetes* Havlíček: 46

TYPE SPECIES. *Strophomena tristis* Barrande, 1879.

DIAGNOSIS. Like *Aegiria* (*Aegiria*), but lacking dental plates.

REMARKS. Havlíček (1967: 47) lists the differences between *Aegiromena* (which we now include in *Aegiria*) and *Aegironetes*. Four of the five differences are either non-existent or only of specific importance, but the absence of dental plates in *Aegironetes*, as opposed to the 'short, divergent' dental plates of *Aegiromena* we consider important enough to warrant subgeneric distinction.

SPECIES ASSIGNED

Aegironetes minuta Xu, Rong & Liu, 1974: 152; pl. 66, figs 9–12, from Shihtzipu Formation (Llandoilo), Zunyi, N. Guizhou Province, China.

Strophomena tristis Barrande, 1879, pars: pl. 70, figs 6:1 (non figs 6:2–4) from Králův Dvůr Formation (L.–M. Ashgill), Kosov, Czechoslovakia (revised Havlíček 1967: 47; pl. 4, figs 17–23).

AEGIRIA (EPELIDOAEGIRIA) Strusz, 1982

1982 *Aegiria* (*Epelidoaegiria*) Strusz: 115

TYPE SPECIES. *Aegiria* (*Epelidoaegiria*) *chilidifera* Strusz, 1982.

DIAGNOSIS. Like *Aegiria* (*Aegiria*) but with hinge line denticulate. Small chilidium present.

REMARKS. Strusz (1982: 115) distinguished *Epelidoaegiria* from *Aegiria* in (a) possessing unequally parvicostellate ornament, (b) possessing a chilidium and (c) in being denticulate. We find that the ornament among plectambonitaceans can be very variable, even within the same subgenus, and discount that feature. The 'chilidium' in *Epelidoaegiria* may better be termed chilidial plates (Strusz 1982: fig. 9 A3) and also occurs in '*Aegiromena*' (Havlíček 1967: 39). However, we regard *Epelidoaegiria* as a valid subgenus of *Aegiria* because of its denticulate hinge line.

SPECIES ASSIGNED

Aegiria (*Epelidoaegiria*) *chilidifera* Strusz, 1982: 116; fig. 9 A–G, 10 A–H from Walker Volcanics (Wenlock), Canberra, Australia.

Stropheodonta minuta Mitchell, 1923: 470; pl. 41, figs 22–25 from Lower Trilobite Bed of Hume Series (Ludlow?), Bowning, New South Wales, Australia.

Aegiria sugiyamai Tachibana, 1976: 37; pl. 5, figs 1–24; pl. 6, figs 3–6; pl. 7, fig. 3 from Kawanchi Series (Wenlock–Ludlow), Kusayami-zawa, Ofunato, Japan.

CHONETOIDEA Jones, 1928

Figs 92, 93, 95

1928	<i>Chonetoidea</i> Jones: 393
1933	<i>Chonetoidea</i> Őpik: 51
1953	<i>Sericoidea</i> Lindström: 134
1957	<i>Chonetoidea</i> Spjeldnaes: 104
1965	<i>Chonetoidea</i> Williams: H383
1965	<i>Sericoidea</i> Williams: H383
1967	<i>Chonetoidea</i> Havlíček: 48
1967	<i>Sericoidea</i> Havlíček: 51
?1967	<i>Sentolunia</i> Havlíček: 53
1970	<i>Chonetoidea</i> Cocks: 192
1977	<i>Chonetoidea</i> Mitchell: 93
1979	<i>Sericoidea</i> Percival: 113
1979	<i>Sericoidea</i> Hurst: 280

TYPE SPECIES. *Plectambonites papillosa* Reed, 1905. Type species of *Sericoidea* is *Leptaena sericea* var. *restricta* Hadding, 1913. Type species of *Sentolunia* is *S. senta* Havlíček 1967, a probable subjective junior synonym of *Chonetes radiatula* Barrande, 1879.

DIAGNOSIS. As for family. Like *Jonesea* gen. nov. but with elongated septules rather than circular papillae. Bema usually absent.

REMARKS. Lindström (1953: 134) differentiated *Sericoidea* from *Chonetoidea* on the basis of 'a slit-like adductor scar' in the pedicle valve which 'has not, as far as I know, been observed in *Chonetoidea*'; however, the adductor scars in *Chonetoidea* are the same when developed. Lindström and Williams (1962: 189; 1965: H383) also separated the two genera on the differentiated ornament of *Sericoidea* as compared with the equal parvicostellae of *Chonetoidea*. However, we have found considerable variation in the ornament, as has Mitchell (1977: 93–94), and also Hurst (1979: 281) 'felt that *Sericoidea* may prove to be a synonym of *Chonetoidea*'. In general there are fewer internal tubercles in *Sericoidea* than *Chonetoidea*, but there is tremendous variation in that character and we cannot separate the two genera. For example, in the population of *Chonetoidea radiatula* figured by Mitchell (1977: pl. 18) the juvenile in fig. 30 shows very

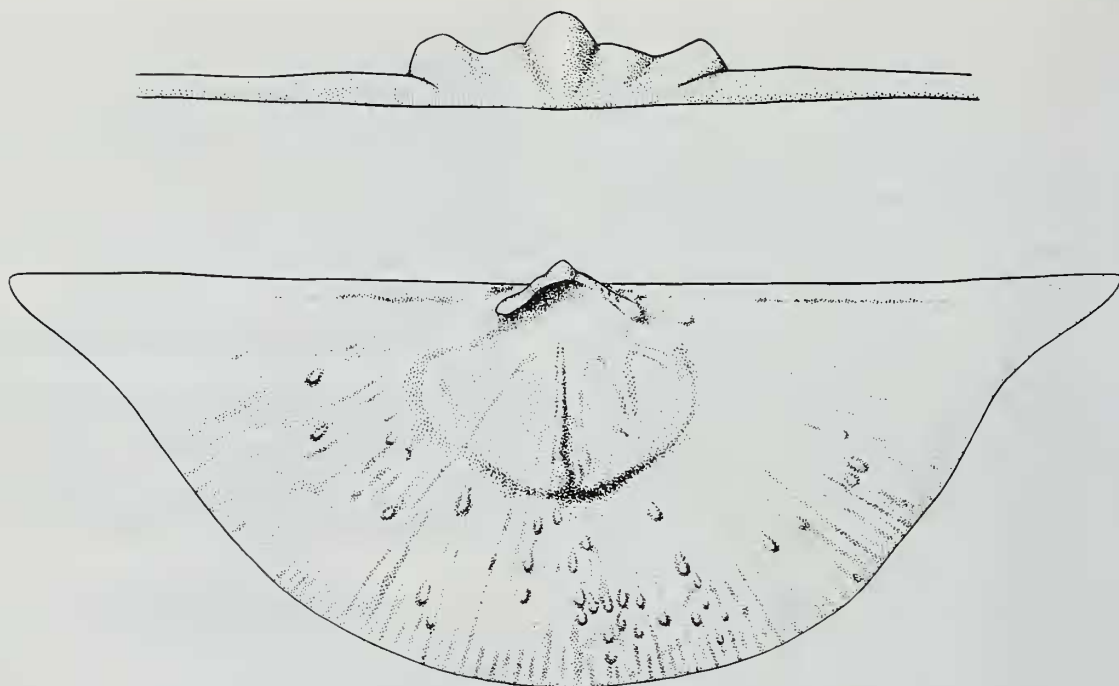


Fig. 94 *Aegiria (Aegiria) aquila aquila* (Barrande, 1848), from Zahoraný Formation (M. Caradoc), Palmovka, Praha-Libeň, Czechoslovakia; a, posterior view of cardinal process, $\times 25$ and b, brachial valve interior, $\times 12$ (based on BC 7212).

few papillae whilst the larger specimen in fig. 24 shows a great number. In addition, some species show many papillae in all their specimens, whilst in other species papillae can be uncommon. Young & Gibbons (1983) also discuss the problem and conclude that *Chonetoidea* and *Sericoidea* should be regarded as synonyms.

Only two specimens are known of *Sentolunia senta* (Havlíček, 1967: 53), one pedicle valve and one brachial valve. In the brachial valve the bema is more obvious and continuous than in the specimens of *Chonetoidea radiatula* from the same formation and locality (Havlíček 1967: pl. 5). We are not certain whether or not *Sentolunia* is correctly synonymized with *Chonetoidea*, but until more specimens become available we think it most likely that these two specimens are at the extreme limit of the range of variation of *Chonetoidea radiatula*.

SPECIES ASSIGNED

Sericoidea abdita Williams, in Whittington & Williams 1955: 418; pl. 39, figs 83–85 from Derfel Limestone (L. Caradoc), Pont Aberderfel, Gwynedd, Wales.

Sericoidea abdita complicata Lockley, 1980: 212, figs 54–59 from Nod Glas Formation (U. Caradoc), Rhiw March, Llanymawddwy, Powys, Wales.

Chonetoidea gamma Spjeldnaes, 1957: 106; pl. 2, figs 12–13 from Zone 4b (Caradoc–Ashgill), Blakstad, Asker, Norway.

Sericoidea homolensis Havlíček, 1967: 52; pl. 8, figs 1–5 from Bohdalec Formation (M. Caradoc), near Kačerov, Czechoslovakia.

Chonetoidea iduna Öpik 1933: 52; pl. 10, figs 6, 7; pl. 11,

figs 1, 2 from Zone 4c (L. Ashgill), Frognö, Ringerike, Norway.

Sericoidea miaopoensis Chang, 1983: 479; pl. 1, figs 7, 14, 15 from Miaopo Formation (U. Llandeilo–L. Caradoc), Huanghuachang, Yichang County, Hubei, China.

Sericoidea minor Percival, 1979: 113, figs 5A, 9–16 from Malongulli Formation (U. Caradoc), Copper Mine Creek, Cheesemans Creek, New South Wales, Australia.

Orthis nina Davidson, 1883: 177; pl. 13, fig. 11 from Whitehouse Group (Caradoc–Ashgill), Whitehouse Bay, Girvan, Scotland.

Plectambonites papillosa Reed, 1905: 451; pl. 23, figs 13–15 from Slade and Redhill Mudstone (M. Ashgill), Haverfordwest, Dyfed, Wales (revised Cocks 1970: 193; pl. 17, figs 1–3).

Chonetes radiatulus Barrande, 1879: pl. 54, fig. 1 from Králův Dvůr Shales (L.–M. Ashgill), Králův Dvůr, Czechoslovakia (revised Havlíček 1967: 49; pl. 5, figs 7–14), a probable subjective senior synonym of *Sentolunia senta* Havlíček 1967: 53; pl. 5, fig. 6 from the same formation and locality; probably also a senior synonym of *Chonetoidea tenerrima* Havlíček 1952: 404; pl. 3, figs 2, 5 (revised Havlíček 1967: 50; pl. 5, figs 1–5) from the same formation at various localities. *C. radiatula* and *C. tenerrima* appear to be large and small individuals of the same population.

Leptaena sericea var. *restricta* Hadding, 1913: 62; pl. 5, figs 29–32 from Lower Chasmops Beds (L. Caradoc), Fågelsång, Scania, Sweden, a senior subjective synonym of *Plectambonites sericea* var. *craigensis* Reed, 1917: 883; pl. 15, figs 12–17 from Craighead Limestone (U. Caradoc), Craighead, Girvan, Scotland (revised Williams 1962: 187; pl. 18, figs 5–9).

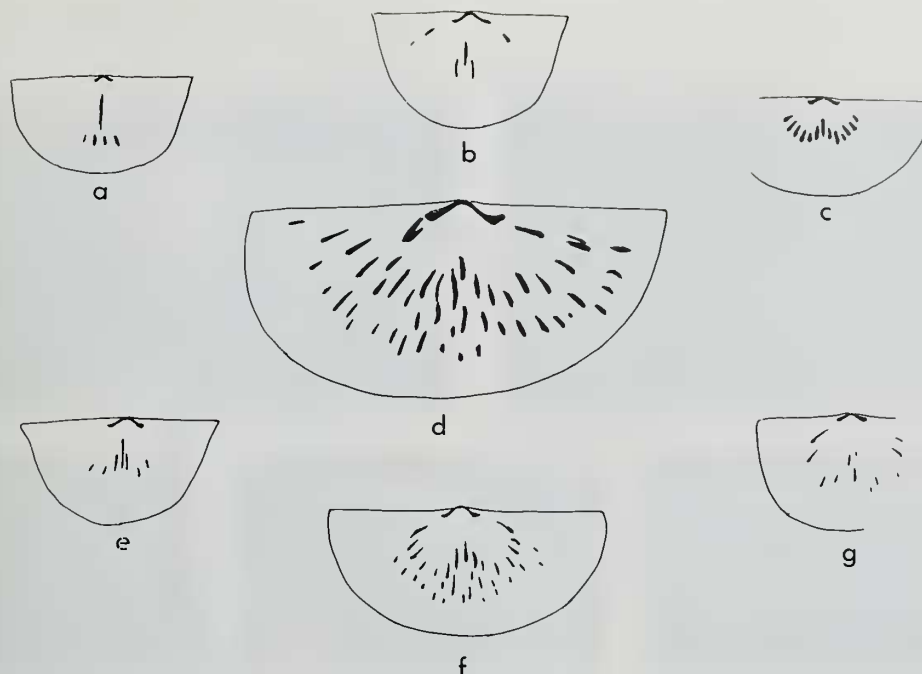


Fig. 95 Brachial valve interiors demonstrating all variants between 'Chonetoidea' and 'Sericoidea'. a, '*Sericoidea*' *minor* Percival, 1979, from Malongulli Formation (U. Caradoc), Copper Mine Creek, New South Wales, Australia (after Percival 1979: fig. 5.A12), $\times 5$; b, '*Chonetoidea*' *enerrima* Havlíček, 1952, from Králův Dvůr Shales (M. Ashgill), Vysebohy, Bohemia, Czechoslovakia (after Havlíček 1967: pl. 5, fig. 3), $\times 7$; c, '*Chonetoidea*' *gamma* Spjeldnaes, 1957, from Zone 4b γ (Caradoc-Ashgill), Blakstad, Oslo, Norway (after Spjeldnaes 1957: pl. 2, fig. 12), $\times 1.5$; d, *Chonetoidea papillosa* (Reed, 1905), from Slade and Redhill Mudstone Formation, Haverfordwest, Wales (after Cocks 1970: pl. 17, fig. 1), $\times 10$; e, '*Chonetoidea*' *virginica* Cooper, 1956, from Edinburg Formation (L. Caradoc), Riverton, Virginia, USA (after Cooper 1956: pl. 215, fig. 33), $\times 5$; f, g, '*Chonetoidea*' *radiatula* (Barrande, 1879), from Killey Bridge Formation (M. Ashgill), Pomeroy, Northern Ireland (after Mitchell 1977: pl. 18, figs 33, 30), $\times 7$ and $\times 8$.

Sericoidea sejuncta Percival, 1979: 113, figs 5A, 1-8 from Goonumbla Volcanics (U. Caradoc), Gunningbland, New South Wales, Australia.

Chonetoidea stoermeri Spjeldnaes, 1957: 108, fig. 24a from Zone 4aa (Llandeilo), Dalbo, Asker, Norway.

Chonetoidea virginica Cooper, 1956: 804; pl. 215, figs 30-33, from Edinburg Formation (L. Caradoc), Riverton, Virginia, USA.

SPECIES QUESTIONABLY ASSIGNED

Leptaena aequistriata Hadding, 1913: 62; pl. 5, figs 27, 28 from *Ogygiocaris* shales (Llanvirn-Llandeilo), Andersön, Scania, Sweden (no interiors illustrated).

Sericoidea hubeiensis Chang, 1983: 480; pl. 1, fig. 26 from U. Miaopo Formation (U. Llandeilo-L. Caradoc), Huanghuachang, Yichang County, Hubei, China.

Chonetoidea mohawkensis Howell, 1949: 7; pl. 2, figs 1-3 from Schenectady Formation (U. Caradoc), Rexford, New York, USA (no interiors illustrated).

Leptaena plicatella Ulrich, 1879: 15; pl. 7, figs 12-12c from Utica Shale with *Triarthrus becki* (M.-U. Caradoc), Cincinnati, Ohio, USA (no interiors known).

Sericoidea shanxiensis Fu, 1982: 118; pl. 34, figs 17-19 from Wufeng Formation (Ashgill), Yuanba, Nanzheng, Shaanxi Province, China (interiors poorly figured but brachial valve appears closer to *Kassinella* rather than *Sericoidea*).

Chonetoidea triangularis Reed, 1932a: 137; pl. 20, figs 8-11 from Hølandet Formation (Caradoc), Katuglåsen, Trondheim, Norway (no interiors known).



Fig. 96 *Jonesea grayi* (Davidson, 1849) gen. nov., interior of brachial valve, based on several specimens from the Ludlow of Shropshire, England, $\times 23$.

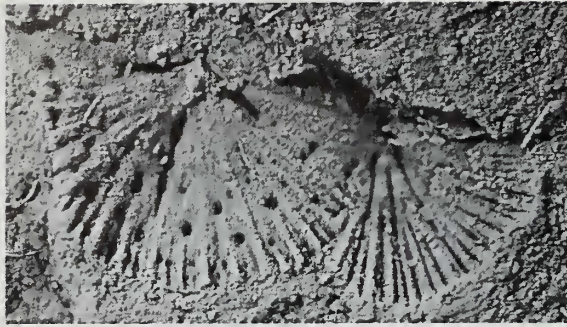
SPECIES REJECTED

Chonetoidea alpha Spjeldnaes, 1957: 107; pl. 2, figs 20-22 from Zone 4ba (U. Caradoc), Billingstad, Asker, Norway (assigned to *Aegiria*).

Chonetoidea (Aegiria) nacta Reed, 1952: 53; pl. 2, fig. 13 from Killey Bridge Formation (L. Ashgill), Pomeroy, Co. Tyrone, Northern Ireland (synonymized with *Sowerbyella thraivensis* Reed by Mitchell 1977: 81).

Chonetoidea garthensis Jones, 1928: 500; pl. 25, figs 25, 26 from Lower Llandovery Beds, N. of Garth, Dyfed, Wales (assigned to *Aegiria*).

Chonetoidea andersoni Johnson, Boucot & Murphy, 1976:



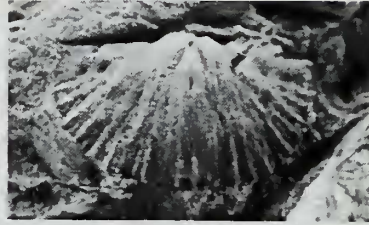
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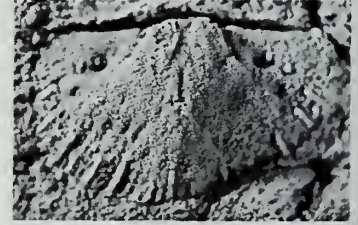
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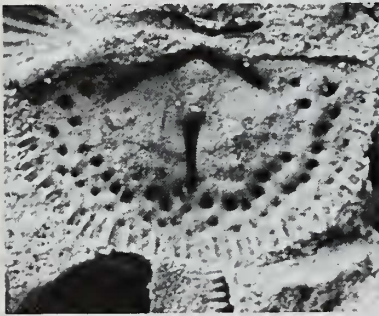
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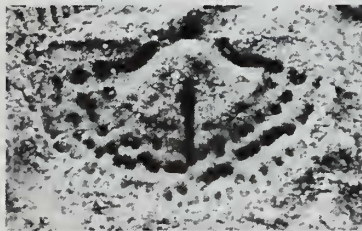
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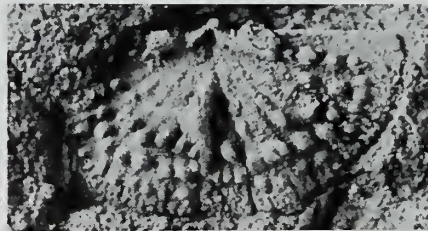
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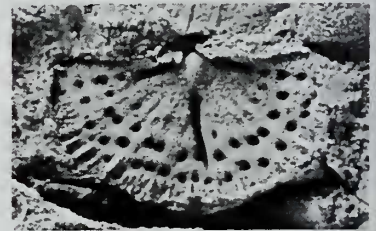
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105



106

Figs 97–106 *Jonesea grayi* (Davidson, 1849) gen. nov. Fig. 97, brachial valve interiors from Purple Shales (U. Llandovery), Onny River, Shropshire, England, OUM C12051–2, $\times 15$; Fig. 98, latex cast of brachial valve interior and pedicle valve exterior from U. Rhydys Formation (M. Llandovery), Cefn Cerig Road, Llandovery, Dyfed, Wales, BB 32128, $\times 12$; Fig. 99, exterior of conjoined valves from Purple Shales (U. Llandovery), Hughley, Shropshire, England, OUM C 13951, $\times 12$; Fig. 100, natural internal mould of pedicle valve from Purple Shales (U. Llandovery), Domas, Shropshire, England, OUM C 13423, $\times 12$; Fig. 101, natural internal mould of pedicle valve from 'Chonetoidea' Beds (M. Ludlow), Pont Shoni, Builth, Powys, Wales, BB 32430, $\times 9$; Fig. 102, natural internal mould and latex cast of a brachial valve from U. Leintwardine Beds (M. Ludlow), Bengry Track, Ludlow, Shropshire, England, BC 10341, $\times 12$; Fig. 103, latex cast of external moulds of conjoined valves from L. Bringewood Beds (U. Ludlow), Bengry track, Ludlow, Shropshire, BC 10343, $\times 12$; Fig. 104, natural internal mould of brachial valve from U. Leintwardine Beds (M. Ludlow), Bengry track, Ludlow, Shropshire, BC 10340, $\times 12$; Fig. 105, latex cast of internal mould of brachial valve from L. Bringewood Beds (U. Ludlow), Bengry track, Ludlow, Shropshire, BC 10375, $\times 12$; Fig. 106, natural internal mould of brachial valve from L. Bringewood Beds (U. Ludlow), Bengry track, Ludlow, Shropshire, BC 10359, $\times 12$.

58; pl. 20, figs 3–25 from Roberts Mountains Formation (Ludlow), Birch Creek, Roberts Mountains, Nevada, USA (to *Jonesea*).

ericoidea postrestricta Kulkov, in Kulkov *et al.* 1985: 75; pl. 8, figs 1, 2 from Kizilchirinski Formation (M.–U. Llandoverly), Chadan Section, Tuva, USSR (brachial valve interior different from *Chonetoidea* but true genus unknown).

JONESEA gen. nov.

Figs 96–106

TYPE SPECIES. *Leptaena grayi* Davidson, 1849. Named after O.T. Jones.

DIAGNOSIS. Like *Chonetoidea*, but with circular papillae rather than elongated. Sometimes septules with 2 prominent tubercles posterolaterally inside the pedicle valve.

REMARKS. Only *Kassinella* and *Trimurellina* within the Plectambonitacea also possess the pair of tubercles sometimes seen within the pedicle valve of *Jonesea* (e.g. Cocks 1970: pl. 7, fig. 13). The bema is usually absent, but is occasionally seen. The type species was previously assigned (e.g. Cocks 1970) to *Aegiria*, but the new genus differs from *Aegiria* in the virtual absence of a bema, as well as in possessing the prominent papillae and tubercles. It seems probable that a systematic reassessment would much reduce the number of real species from the nominal list below.

SPECIES ASSIGNED

Chonetoidea andersoni Johnson, Boucot & Murphy, 1976: 58; pl. 20, figs 3–25 from Roberts Mountain Formation (Ludlow), Birch Creek, Roberts Mountains, Nevada, USA.

Aegiriomena durbenensis Nikitin, in Nikitin *et al.* 1980: 52; pl. 13, figs 16–22 from Durben Formation (U. Ashgill), Durben, Chu-Ili Mountains, Kazakhstan, USSR.

Leptaena grayi Davidson, 1849: 271; figs 1, 1a from Much Wenlock Limestone (U. Wenlock), Dudley, West Midlands, England (revised Cocks 1970: 197; pl. 17, figs 8–14).

Aegiriomena incerta Wan, 1982: 41; pl. 11, figs 19, 20 from Shihniulan Formation (U. Llandoverly), Guanyinqiao, Oijiang County, Sichuan Province, SW China.

Chonetoidea luoheensis Su, 1980: 270; pl. 116, figs 5–10 from Luohe Formation (U. Ordovician), east side of Luohe River, Aihui County, Heilongjiang Province, NE China.

Aegiria mariaformis Lenz, 1677a: 67; pl. 8, figs 6–9, 12–21, from L. Road River Formation (Pridoli), Royal Creek, Yukon, Canada.

Aegiria cf. *mariaformis* Lenz, 1977b: 1536; pl. 5, figs 19, 22–28 from U. Whittaker Formation (Wenlock), Avalanche Lake, Mackenzie Mountains, Canada.

Aegiria mongoliensis Alekseeva, in Alekseeva & Erlanger 1983: 28; pl. 6, figs 5–10; pl. 12, figs 6–9 from Middle Silurian, River Yarmaty-Gol, NW Mongolia.

Orthis myrmido Barrande, 1879: pl. 64, fig. 1; pl. 127, fig. 7–1 from Litéň Formation (Wenlock), Dlouhá hora hill, near Beroun, Czechoslovakia (revised Havlíček 1967: 46; pl. 3, figs 15, 16).

Aegiriomena praeultima Mikuláš, 1983: 5; pl. 1, figs 1–9 from Podolí iron ore horizon, Králův Dvůr Formation (L.–M. Ashgill), Vlnitá ulice, Praha-Braník, Czechoslovakia.

Aegiria thomasi Talent, 1965: 24; pl. 6, figs 1, 3, 5–7 from Dargile Formation (Ludlow), Heathcote, Victoria, Australia.

Aegiriomena ultima Marek & Havlíček, 1967: 281; pl. 3, figs 9–12 from Kosov Formation (U. Ashgill), Běchovice, Czechoslovakia.

Aegiriomena yanheensis Rong & Yang, 1981: 171; pl. 2, figs 17–25 from Leijiatuan Formation (U. Llandoverly), Ganxi, Yanhe County, NE Guizhou Province, China.

Aegiria sp. of Fu, 1982: 119; pl. 34, fig. 20 from Zhouqu Group (Wenlock), Xiaolianggou, Miaogou, Zhouqu County, Gansu Province, N. China (very similar to *J. mariaformis*).

SPECIES QUESTIONABLY ASSIGNED

Plectodonta aknistensis Rybnikova, 1967: 188; pl. 19, figs 1, 2 from L. Ludlow borehole in Latvia, USSR (no interiors known but exteriors the same as *Jonesea*).

Plectambonites aequalis Teichert, 1928: 58; pl. 5, figs 18–20 from Tamsal Formation (L.–M. Llandoverly), Kiltsi, Estonia, USSR (only brachial valve interior figured is not clear in detail, but the pedicle valve external figured shows *Jonesea*-like ornament).

Sowerbyella austrum Öpik, 1953: 14; pl. 3, figs 17, 18 from Wapentake Formation (U. Llandoverly), Heathcote, Victoria, Australia (almost certainly assigned, but no brachial interior known).

MEZOUNIA Havlíček, 1967

1967 *Mezounia* Havlíček: 31

TYPE SPECIES. *Strophomena bicuspis* Barrande, 1879.

DIAGNOSIS. Like *Aegiria* but with bema bilobed anteriorly.

REMARKS. This genus was previously assigned by Havlíček (1967) to the Leptestiinidae, but the cardinal process is undercut (Havlíček 1967: pl. 2, fig. 14) and thus *Mezounia* is placed here within the Aegiriomeninae.

SPECIES ASSIGNED

Strophomena bicuspis Barrande, 1879: pl. 128, figs 1–5 from Litéň Formation (Wenlock), Loděnice, Czechoslovakia (revised Havlíček 1967: 31; pl. 2, figs 7–10, 13–15).

Family *HESPEROMENIDAE* Cooper, 1956

1956 Hesperomeninae Cooper: 744

1963 Anoptambonitidae Rõõmusoks: 231

1967 Anoptambonitidae Havlíček: 35

1979 Anoptambonitidae Percival: 94

DIAGNOSIS. Cardinal process undercut. No bema. No side septa. With platform.

REMARKS. Although *Hesperomena* is based on only one specimen, nevertheless Cooper (1956: pl. 185) was able to illustrate both the external and internal details of both valves and the genus does not differ enough from *Anoptambonites* to allow us to separate them into two different families. In the *Treatise* (Williams 1965: H373), *Hesperomena* is allocated to the Leptestiinae, but there is no doubt from Cooper's illustrations and descriptions that it possesses an undercut cardinal process, which immediately separates it from *Leptestia* and its allies. Therefore, we are forced to promote Cooper's subfamily. Hesperomeninae to familial rank, which is a senior synonym of the Anoptambonitidae.

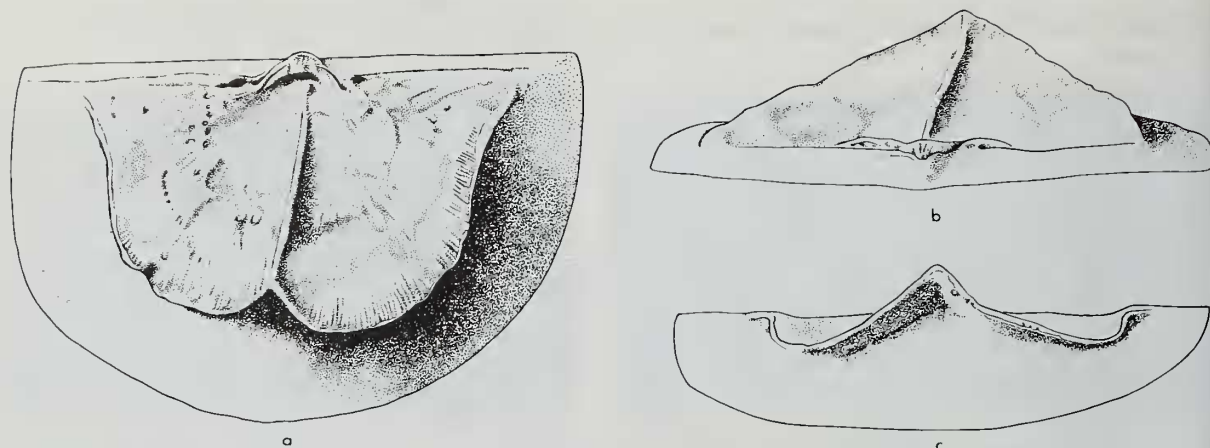


Fig. 107 *Anoptambonites grayae* (Davidson, 1883), downwards, posterior and anterior views of the brachial valve interior, from Craighead Limestone (U. Caradoc), Craighead, Girvan, Strathclyde, Scotland (based on BB 15869), $\times 2.5$.

GENERA ASSIGNED. *Anoptambonites* Williams, 1962 (including *Chaganella* Nikitin, 1974); *Aulie* Nikitin & Popov, 1984; *Hesperomena* Cooper, 1956; *Kassinella* (*Kassinella*) Borriassiak, 1956 (including *Durranelina* Percival, 1979); *Kassinella* (*Tri-murellina*) Mitchell, 1977.

RANGE. U. Llanvirn (*Hesperomena leptellinoidea*) to M. Ashgill (*Kassinella moneta*).

ANOPTAMBONITES Williams, 1962
Figs 107–111

- 1962 *Anoptambonites* Williams: 170
1963 *Anoptambonites* Rõmusoks: 233 *pars*
1965 *Anoptambonites* Williams: H376
1974 *Chaganella* Nikitin: 65

TYPE SPECIES. *Leptaena grayae* Davidson, 1883. The type species of *Chaganella* is *C. chaganensis* Nikitin, 1974.

DIAGNOSIS. Cardinal process striated posteriorly. With elevated platform. Small pedicle valve muscle scars restricted by bilobed muscle boundary ridges. No pedicle valve median septum. No posterolateral tubercles in ventral valve. With chilidium.

REMARKS. We can find no important points of difference in the morphologies of *Anoptambonites* and *Chaganella*, although Nikitin (1974) did not compare them, and thus we synonymize the two genera here.

SPECIES ASSIGNED

- Chaganella chaganensis* Nikitin, 1974: 66; pl. 6, figs 11–17 from L. Bestamak Formation (Llandeilo), Chagan River, Chinghiz Mountains, Kazakhstan, USSR.
Leptaena grayae Davidson, 1883: 171; pl. 12, figs 23–25 from Craighead Limestone (U. Caradoc), Craighead, Girvan, Scotland (revised Williams 1962: 171; pl. 16, figs 11–14, 17).
Anoptambonites grayae sibirica Severgina 1984b: 40; pl. 3, figs 6–11 from Chakirksi horizon (Ashgill), Gornoi Altai Mountains, USSR.
Anoptambonites orientalis Popov, 1980b: 149; pl. 2, figs 12–17 from Anderkensi horizon (U. Llandeilo–L. Caradoc), Anderken-Akchok, Chu-Ili Mountains, Kazakhstan, USSR.
Anoptambonites cf. *A. grayae* of Ross & Dutro 1966: 12; pl. 2, figs 1, 3, 5, 7, 9 from beds of Caradoc age, Hard Luck Creek, Alaska, USA.
Anoptambonites sp. of Mitchell 1977: 73; pl. 13, figs 21, 22, 24–29 from Killey Bridge Formation (L. Ashgill), Killey Bridge, Pomeroy, Northern Ireland.

SPECIES QUESTIONABLY ASSIGNED

- Anoptambonites aktasensis* Nikitin & Popov, 1984: 147; pl. 18, figs 17–23 from Erkebinanski Horizon (Caradoc), Chinghiz Mountains, Kazakhstan, USSR (has pedicle valve platform and median septum in the brachial valve is much wider than in other *Anoptambonites*).

Fig. 108 *Anoptambonites* sp., natural internal mould of pedicle valve, the original of Williams 1962: pl. 16, fig. 10, from Balclatchie Conglomerate (L. Caradoc), Penwhapple Burn, Girvan, Strathclyde, Scotland, BB 25950, $\times 4$.

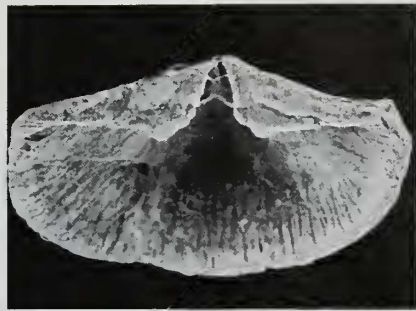
Figs 109–111 *Anoptambonites grayae* (Davidson, 1883), topotypes from Craighead Limestone (U. Caradoc), Craighead, Girvan, Strathclyde, Scotland. Fig. 109, posterior and downward views of a pedicle valve interior, the original of Williams 1962: pl. 16, figs 11, BB 15868, $\times 3.5$; Fig. 110, brachial valve interior, the original of Reed 1917: pl. 13, fig. 16, B 73410, $\times 3$; Fig. 111, brachial valve interior, the original of Williams 1962: pl. 16, fig. 13, BB 15869, $\times 3.5$.

Figs 112–114 *Kassinella* (*Kassinella*) sp. from China. Fig. 112, natural internal mould of brachial valve from L. Miapo Formation (Llandeilo), Huanghuachang, Yichang County, Hubei Province, BC 3307, $\times 14$; Figs 113, 114, latex cast of brachial valve interior and natural internal mould of pedicle valve interior from Changwu Formation (M. Ashgill), hill to west of Jiangshan County, SW Zhejiang Province, NIGP 101836 and NIGP 101834, $\times 10$.

Figs 115–117 *Kassinella* (*Kassinella*) *albida* (Reed, 1917), from Whitehouse Beds (Caradoc–Ashgill), Whitehouse Bay, Girvan, Strathclyde, Scotland. Fig. 115, natural internal moulds of conjoined valves, BB 92584, $\times 10$; Fig. 116, natural internal mould of brachial valve, BB 92573, $\times 10$; Fig. 117, natural internal mould of brachial valve, lectotype, selected Cocks 1978: 96, the original of Reed 1917: pl. 14, fig. 46, B 73542, $\times 10$.



108



109a



109b



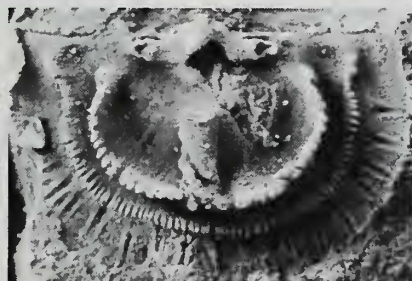
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111



112



113



114



115



116



117

Rafinesquina carinata Holtedahl, 1916: 25; pl. 2, figs 4, 5 from 5a beds (M. Ashgill), Stavnaestangen, Ringerike, Norway. (No interiors figured by Holtedahl, but assigned to genus without illustrations by Rõõmusoks 1963: 233 and Havlíček 1967: 35).

SPECIES REJECTED

'*Anoptambonites*' *incertus* Xu, Rong & Lui, 1974: 153; pl. 66, figs 5, 6 from Chientsaokou Formation (L. Ashgill), Zunyi, N. Guizhou Province, China (allocated here to *Kassinella*).

Anoptambonites pirguensis Rõõmusoks, 1963: 233; pl. 1, figs 1-4 from Pirgu Formation (M. Ashgill), Pirgu River, Estonia, USSR (differs from *Anoptambonites* in brachial valve median septum being joined posteriorly to cardinal process and not reaching platform anteriorly; pedicle interior unknown: the true generic assignment requires re-investigation of a topotype population).

Strophomena quaesita Barrande, 1879: pl. 127, figs 2-3 from Králův Dvůr Shales (Ashgill), Kosov, Czechoslovakia (assigned to *Anoptambonites* by Havlíček 1967: 36; pl. 2, figs 17, 19, but subsequently made the type species of *Proboscisambon* Havlíček & Mergl, 1982 and reassigned to the Strophomenacea by Cocks & Rong 1988).

AULIE Nikitin & Popov, 1984

1984 *Aulie* Nikitin & Popov: 148

TYPE SPECIES. *Aulie convexa* Nikitin & Popov, 1984.

DIAGNOSIS. Like *Anoptambonites* but with brachial valve median septum extending a little anteriorly of platform and with pedicle valve muscle bounding ridges semicircular, not bilobed.

REMARKS. The length of the median septum in *Aulie* is variable anteriorly and if this feature was the only character distinguishing it from *Anoptambonites* then we would synonymize the two genera or consider them as two separate subgenera. However, the different shapes of the pedicle valve muscle field enables us still to treat them as separate.

SPECIES ASSIGNED

Aulie convexa Nikitin & Popov 1984: 149; pl. 17, figs 1-9 from Erkebidaiski horizon (U. Caradoc), Chinghiz Mountains, Kazakhstan, USSR.

HESPEROMENA Cooper, 1956

1956 *Hesperomena* Cooper: 744

1965 *Hesperomena* Williams: H373

TYPE SPECIES. *Hesperomena leptellinoidea* Cooper, 1956.

DIAGNOSIS. With weak platform. Large muscle scars in the pedicle valve.

REMARKS. *Hesperomena* differs from *Anoptambonites* in the lack of elevated platform and lack of bilobed muscle-bounding ridges in the pedicle valves. There are no posteriorly striated cardinal process or posterolateral tubercles in the pedicle valve.

SPECIES ASSIGNED

Hesperomena leptellinoidea Cooper 1956: 745; pl. 185, figs 1-

10 from Antelope Valley Limestone, Pogonip Group (U. Llanvirn), Ikes Canyon, Roberts Mountains, Nevada, USA.

KASSINELLA (KASSINELLA) Borissiak, 1956

Figs 112-119

1956 *Kassinella* Borissiak: 50

1965 *Kassinella* Williams: H383

1979 *Durranelia* Percival: 96

1979 *Kassinella* Percival: 101

1984 *Kassinella* Klenina: 86

TYPE SPECIES. *Kassinella globosa* Borissiak, 1956. Type species of *Durranelia* is *D. septata* Percival, 1979.

DIAGNOSIS. Like *Aulie* but with peripheral rim developed and pedicle valve muscle-bounding ridges bilobed. Median septum well beyond platform, meeting, but not extending anteriorly of, the peripheral rim. No dental plates. Like *Trimurellina* but with brachial valve median septum not extending anteriorly of the platform. Peripheral rim variably developed. Posterolateral tubercles usually present in pedicle valve. Median septum always present in pedicle valve.

REMARKS. Percival (1979: 96) separated *Durranelia* from *Kassinella* on the absence of posterolateral tubercles in the pedicle valve; however, these tubercles can be seen on the pedicle valve of both species of *Durranelia* (e.g. Percival 1979: fig. 3A: 1, 2, 10, 11). In addition Percival said that the peripheral rim typical of *Kassinella* is only 'exceptionally and poorly' developed in *Durranelia*, but the fact that it sometimes occurs does not enable us to separate the two genera. The peripheral rim is very variable in the type population of *Kassinella albida* (Reed), illustrated here (Figs 115-117) and is partly dependent on ontogeny. Even in the type species, *Kassinella globosa* (Borissiak 1956: 50; pl. 12, figs 1c, 6) the peripheral rim is not developed.

SPECIES ASSIGNED

Plectambonites sericea var. *albida* Reed, 1917: 882; pl. 14, figs 42-46; pl. 15, figs 1-3 from Whitehouse Group (L. Ashgill), Whitehouse Bay, Girvan, Scotland.

Kassinella anisa Percival, 1979: 101, figs 5B: 1-3, 7A: 1-8 from Goonumbla Volcanics (U. Caradoc), Gunningbland, New South Wales, Australia.

Kassinella globosa Borissiak, 1956: 51; pl. 12, figs 1-7 from Ashgill Beds, Uly-Tay, Dzhzhkazganski region, Kazakhstan, USSR.

'*Anoptambonites*' *incertus* Xu, Rong & Liu 1974: 153; pl. 66, figs 5, 6 from Chientsaokou Formation (L. Ashgill), Zunyi N. Guizhou Province, China.

Strophomena moneta Barrande, 1879: pl. 57, fig. 6 from Králův Dvůr Formation (M. Ashgill), Kosov, Bohemia Czechoslovakia (revised by Havlíček 1967: 35; pl. 2, figs 1-6 as *Anoptambonites moneta* including junior synonym *Orthis humillima* Barrande, 1879: pl. 69, fig. V-1 from the same horizontal locality).

Kassinella nana Klenina, 1984: 87; pl. 7, figs 2, 10; pl. 8, figs 20-27 from Taldiboiskaya Formation, bed tb_{iii} (Ashgill) River Taldiboi, Chinghiz Mountains, Kazakhstan, USSR.

Durranelia rugosa Percival, 1979: 99, figs 3A: 10-20 from L Malongulli Formation (L. Ashgill), Cliefden Caves, New South Wales, Australia.

Durranelia septata Percival 1979: 97, figs 3A: 1-9 from Goonumbla Volcanics (U. Caradoc), Gunningbland, New South Wales, Australia.

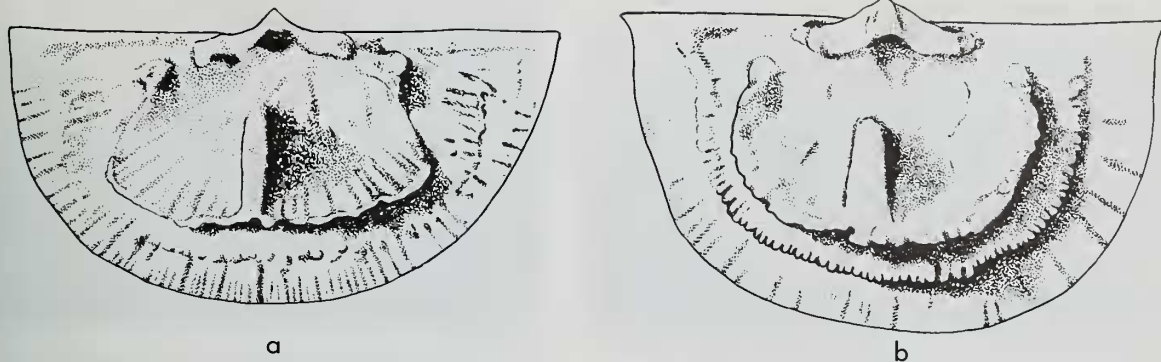


Fig. 118 *Kassinella (Kassinella)* sp. showing variation in the brachial valve interior from a population in the Changwu Formation (M. Ashgill), Jiangshan County, SW Zhejiang Province, China: a, after NIGP 101835, $\times 12$; b, after NIGP 101836, $\times 12$.

Chonetoidea simorini [Borissiak MS] Sokolskaya, 1960: pl. 27, figs 24, 25 from Middle Ordovician, N. Kazakhstan, USSR.

Anoptambonites sp. of Sheehan 1973: 62; pl. 2, figs 1, 2 from Jerrestad Mudstone (L. Ashgill), Fågelsång, Scania, Sweden.

SPECIES QUESTIONABLY ASSIGNED

Kassinella tschinghisensis Klenina, 1984: 87; pl. 8, figs 1–6 from Taldiboiskaya Formation, Bed tb_{iv} (Ashgill), River Taldiboi, Chinghiz Mountains, Kazakhstan, USSR (no interiors figured).

KASSINELLA (TRIMURELLINA) Mitchell, 1977

Figs 120–123

977 *Trimurellina* Mitchell: 74

TYPE SPECIES. *Trimurellina superba* Mitchell, 1977.

DIAGNOSIS. Like *Kassinella (Kassinella)* but with brachial valve median septum extending anteriorly of the platform.

REMARKS. As stated in the remarks on *Kassinella (Kassinella)*, the sub-peripheral rim is variably developed, but it is usually present in *K. (Trimurellina)* (except for the two specimens illustrated in Mitchell 1977: pl. 14, figs 3, 4). The brachial valve median septum is also variable in length, but only in *K. (Trimurellina)* does it regularly extend anteriorly beyond the platform, which is the basis for retaining a separate subgenus.

SPECIES ASSIGNED

Trimurellina superba Mitchell, 1977: 74; pl. 14, figs 1–16 from Killey Bridge Formation (L.–M. Ashgill), Killey Bridge, Pomeroy, Northern Ireland.

SPECIES QUESTIONABLY ASSIGNED

Trimurellina sp. of Williams & Wright 1981: 12, fig 4A from Wenallt Formation (Upper Ashgill), Wenallt, Garth, Powys, Wales.

Family **SOWERBYELLIDAE** Öpik, 1930

- 1930 Sowerbyellinae Öpik: 60
- 1938 Sowerbyellinae Ulrich & Cooper: 186
- 1953 Sowerbyellinae Williams: 8
- 1956 Sowerbyellidae Cooper: 774
- 1965 Sowerbyellidae Williams: H378 *pars*
- 1967 Sowerbyellidae Havlíček: 37 *pars*
- 1967 Dubioleptinidae Havlíček: 70
- 1970 Sowerbyellidae Cocks: 164

DIAGNOSIS. Undercut cardinal process. With side septa. With bema usually developed.

REMARKS. A bema is usually present in species assigned to this family, although it becomes better developed and thicker in gerontic individuals and is very often not seen in young specimens. In a few species it is not developed at all, for example in *Sowerbyella sinensis*, which on all other grounds

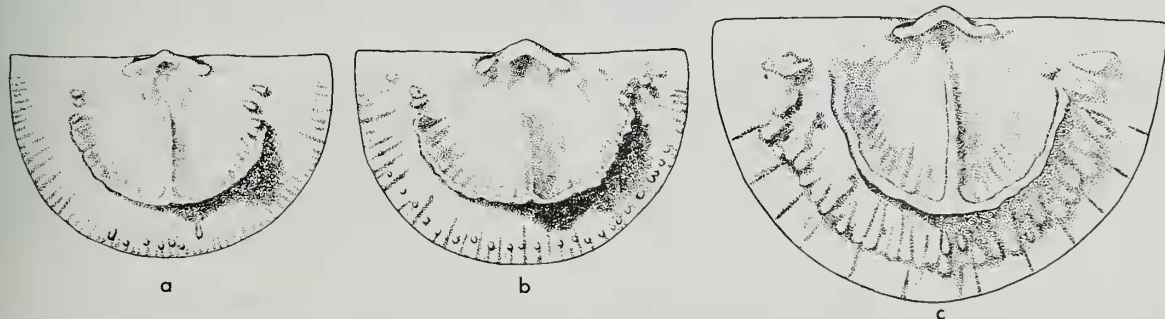


Fig. 119 *Kassinella (Kassinella) albida* (Reed, 1917), showing variation in the brachial valve interior in the topotype population from Whitehouse Beds (Caradoc–Ashgill), Whitehouse Bay, Girvan, Strathclyde, Scotland: a, after BB 92584; b, after BB 92573; c, after B 73542, the lectotype, all $\times 8$.



120



121



122



123

Figs 120–123 *Kassinella (Trimurellina) superba* Mitchell, 1978, from Killeen Bridge Formation (M. Ashgill), Pomeroy, Co. Tyrone, Northern Ireland. Fig. 120, natural internal mould of brachial valve, holotype, the original of Mitchell 1978: pl. 14, figs 5, 6, GSM GU 1109, $\times 18$; Fig. 121, natural internal mould of pedicle valve, the original of Mitchell 1978: pl. 14, fig. 14, GSM GU 1113, $\times 20$; Fig. 122, natural internal mould of brachial valve, the original of Mitchell 1978: pl. 14, fig. 3, GSM GU 1121, $\times 20$; Fig. 123, natural internal mould of brachial valve, the original of Mitchell 1978: pl. 14, fig. 7, GSM GU 1124, $\times 20$.

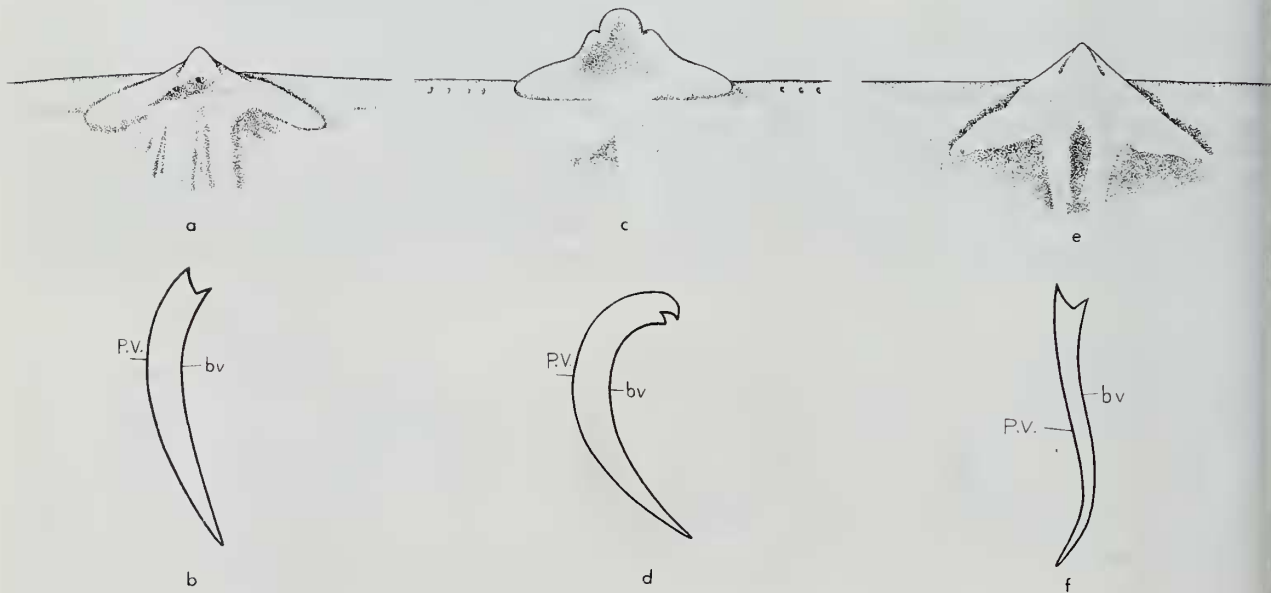


Fig. 124 Variation in the cardinal process and valve shape amongst various genera of Sowerbyellinae: a, b, *Sowerbyella eximia* Cooper, 1956 from Martinsburg Formation (L. Caradoc), Virginia, USA; c, d, *Eoplectodonta duvalii* (Davidson, 1847), from Slite Marl (Wenlock), Gotland Sweden; e, f, *Gunningblandella resupinata* Percival, 1979, from Goonumbla Volcanics (U. Caradoc), New South Wales, Australia.

can be unequivocally assigned to *Sowerbyella*. In most of the species of *Sowerbyella* itself, including *S. sericea* the type species, the bema is well developed. The family is divided into three subfamilies on the division of the bema and whether or not the cardinal process is differentiated into a separate recognizable structure, or whether, as in the *raspedeliinae*, it is totally fused and inseparable from the other central structures on the brachial valve hinge line.

SUBFAMILIES ASSIGNED. Sowerbyellinae Öpik, 1930; Craspedeliinae subfam. nov.; Ptychoglyptinae Cooper, 1956.

RANGE. Llanvirn to Eifelian.

Subfamily SOWERBYELLINAE Öpik, 1930

- 965 Sowerbyellinae Williams: H378
 967 Sowerbyellinae Havlíček: 54
 970 Sowerbyellinae Cocks: 164

DIAGNOSIS. Bema divided. Cardinal process differentiated.

GENERA ASSIGNED. *Anisopleurella* Cooper, 1956; *Dubioleptina* Havlíček, 1967; *Eoplectodonta* (*Eoplectodonta*) Kozłowski, 1929, including *Ygera* Havlíček, 1961; *Eoplectodonta Ygerodiscus* Havlíček, 1967; *Eoplectodonta* (*Kozłowskites*) Havlíček, 1952; *Gunningblandella* Percival, 1979; *Plectodonta* (*Plectodonta*) Kozłowski, 1929; *Plectodonta* (*Plectodontella*) Havlíček, 1953; *Plectodonta* (*Dalejodiscus*) Havlíček, 1961; *Sowerbyella* (*Sowerbyella*) Jones, 1928, including *Viruella* Rõõmusoks, 1959; *Sowerbyella* (*Eochonetes*) Reed 1917, including *Thaerodonta* Wang, 1949; *Sowerbyella* (*Rugosowerbyella*) Mitchell, 1977.

RANGE. Llanvirn (*Sowerbyella antiqua*) to Eifelian (*Plectodonta comitans* and others).

ANISOPLEURELLA Cooper, 1956

Figs 125–127

- 956 *Anisopleurella* Cooper: 804
 965 *Anisopleurella* Williams: H380
 970 *Anisopleurella* Cocks: 189

TYPE SPECIES. *Anisopleurella tricostellata* Cooper, 1956.

DIAGNOSIS. Prominent lateral side septa confined within suboval bema. No denticles on hinge line. Bema usually shorter than in *Eoplectodonta*. Median septum present in brachial valve. Like *Sowerbyella* but no prominent paired central side septa developed.

REMARKS. Cocks (1970: 190) drew attention to the presence of 'very faint crenulations' on the hinge line of some specimens of *A. gracilis*. Nevertheless, because of the very sporadic occurrence of these structures, we do not propose to recognize them generically; in particular we have not seen them on topotype specimens of *A. tricostellata* (Figs 125, 126), kindly presented in exchange by Dr G. A. Cooper.

SPECIES ASSIGNED

Plectambonites quinquecostata var. *balclatchiensis* Reed, 1917: 877; pl. 14, figs 4–9 from Balclatchie Mudstones (L. Caradoc), Balclatchie, Girvan, Scotland (revised Williams 1962: 185; pl. 17, figs 36, 37, 40, 41; pl. 18, figs 1–3), a senior synonym of *P. q. sublobata* Reed, 1917: 879; pl. 14,

figs 10, 20–23 and of *Plectambonites praeteritus* Reed, 1945: 312; pl. 1, fig. 4, both from the same horizon and locality. *Sowerbyella gracilis* Jones, 1928: 472; pl. 24, figs 21–25 from L. Haverford Mudstone Fm (U. Ashgill–L. Llandovery), Haverfordwest, Dyfed, Wales (revised Cocks 1970: 189; pl. 16, figs 1–9; Temple 1970: 38; pl. 8, figs 4–7, 10–13 and Temple 1987: 58; pl. 5, figs 9–15).

Anisopleurella inaequistriata Cooper, 1956: 805; pl. 193, figs 5–9 from M. Whitesburg Formation (Llandoilo), Bulls Gap, Tennessee, USA.

Eoplectodonta karina Spjeldnaes, 1957: 100; pl. 3, fig. 5 from 4ba Beds (M. Caradoc), south end of Nakholmen, Oslo, Norway.

Sowerbyella multiseptata Williams, in Whittington & Williams 1955: 416, figs 74–78 from the Derfel Limestone (L. Caradoc), Derfel, Gwynedd, Wales.

Anisopleurella novemcostata Nikitin, in Nikitin *et al.* 1980: 50; pl. 13, figs 13–15 from Durben Formation (U. Ashgill), Durben Well, Chu-Ili Mountains, Kazakhstan, USSR.

Anisopleurella ovalifera Havlíček, 1967: 55; pl. 6, figs 8, 9 from the Králův Dvůr Shales (Ashgill), Praha-Spořilov, Czechoslovakia.

Anisopleurella tricostellata Cooper, 1956: 806; pl. 193, figs 1–4; pl. 195, figs 1–5 from Pratt Ferry Formation (Llandoilo), Pratt Ferry, Alabama, USA.

SPECIES QUESTIONABLY ASSIGNED

Anisopleurella anceps Mitchell 1977: 86; pl. 17, figs 9–19 from Killey Bridge Formation (Ashgill), Killey Bridge, Pomeroy, Northern Ireland (if the specimens figured by Mitchell 1977: pl. 17, figs 14, 17, 18 possess denticles, then the species should be transferred to *Eoplectodonta*).

DUBIOLEPTINA Havlíček, 1967

- 1967 *Dubioleptina* Havlíček: 70

TYPE SPECIES. *Strophomena expulsa* Barrande, 1879.

DIAGNOSIS. Like *Sowerbyella* but with no socket plates. Hinge line not denticulate.

REMARKS. Although only two brachial valve internals are known, they clearly lack the socket plates of *Eoplectodonta*, which separates *Dubioleptina* from that genus. However, we do not agree with the familial difference which Havlíček feels warranted because the arrangement of the valves is generally reminiscent of *Eoplectodonta*, and in the shales in which *Dubioleptina* is found the socket plates may not have been preserved.

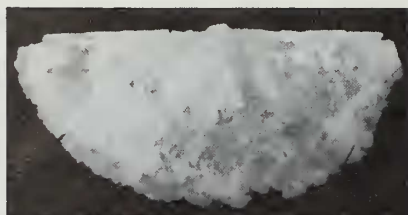
SPECIES ASSIGNED

Strophomena expulsa Barrande, 1879: pl. 53, fig. 4 from U. Liteň Formation (Wenlock), Lodeniče, Czechoslovakia (revised Havlíček 1967: 71; pl. 2, figs 11, 12; pl. 9, figs 11, 14–19; pl. 51, figs 2, 6), and its junior synonym *Strophomena plicatilis* Barrande, 1879: pl. 48, fig. 2 from the same horizon and locality.

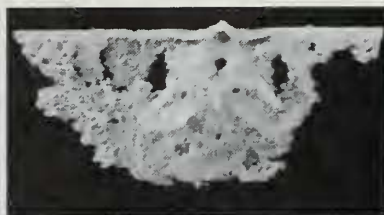
EOPLECTODONTA (EOPLECTODONTA) Kozłowski, 1929

Figs 128–137

- 1929 *Plectodonta* (*Eoplectodonta*) Kozłowski: 112
 1956 *Eoplectodonta* Cooper: 807



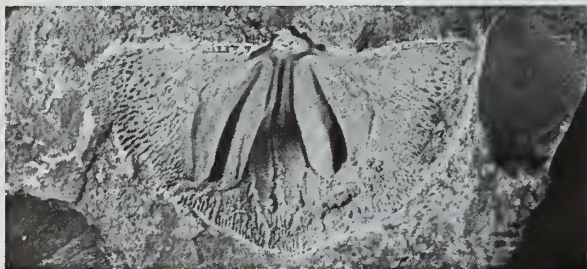
125



126



127



128



129



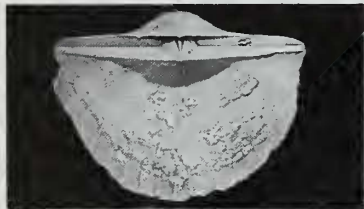
130a



130b



130c



131



132



133



134



135



136

Figs 125, 126 *Anisopleurella tricostellata* Cooper, 1956, from Pratt Ferry Formation (Llandeilo), SE of Pratt Ferry, Blocton, Alabama, USA.

Fig. 125, exterior view of silicified pedicle valve, BB 32855, $\times 7$; Fig. 126, interior of silicified brachial valve, BB 32856, $\times 7$.

Figs. 127 *Anisopleurella* sp., internal mould of brachial valve from the L. Miaopo Formation (Llandeilo), Huanghuachang, Yichang County, Hubei Province, China, BC 3305, $\times 6$.

Fig. 128, 129 *Eoplectodonta duplicata* (J. de C. Sowerby, 1839), from U. Haverford Mudstone Formation (L. Llandovery), lane opposite Gasworks, Haverfordwest, Dyfed, Wales; Fig. 128, internal mould of brachial valve, BB 31670, $\times 3$; Fig. 129, latex cast of internal mould of brachial valve, BB 31693, $\times 3$.

Fig. 130 *Eoplectodonta duvalii* (Davidson, 1847), a brachial valve from Slite Marl (Wenlock), 1.6 km south of church at Västergarn, Gotland, Sweden, the original of Cocks 1970: pl. 12, figs 14, 15, BB 31837; a, viewed posteriorly, $\times 4$; b, c, viewed downwards and laterally, $\times 3$.

Figs 131–136 *Eoplectodonta transversalis* (Wahlenberg, 1818), from L. Visby Marl (U. Llandovery). Figs 131–3 and 136 from beach 1 km west of Lundbjars, Figs 134–5 from beach north of Nyhamn, all north of Visby, Gotland, Sweden. Fig. 131, brachial view of conjoined valves, BB 34810, $\times 3$; Fig. 132, slightly inclined view of pedicle valve interior, the original of Cocks 1970: pl. 12, fig. 12, BB 32423, $\times 3$; Figs 133–6, all interiors of brachial valves, showing variations in the bema and even an incipient platform in Fig. 136; Fig. 133, BB 34826; Fig. 134, BB 34846; Fig. 135, BB 34847; Fig. 136, BB 34827; all $\times 3$.

- 961 *Ygera* Havlíček: 449
 965 *Eoplectodonta* Williams: H380 *pars* (*non*
Thaerodonta)
 967 *Ygera* Havlíček: 58
 970 *Eoplectodonta* Cocks: 166

TYPE SPECIES. *Sowerbyella precursor* Jones, 1928, a junior subjective synonym of *Leptaena duplicata* J. de C. Sowerby, 839. The type species of *Ygera* is *Y. ygerens* Havlíček, 1961.

DIAGNOSIS. Like *Sowerbyella* but with denticulate hinge line on pedicle valve and corresponding fossettes in the brachial valve hinge line.

REMARKS. Havlíček (1967: 58) differentiated *Eoplectodonta* with a median septum in the brachial valve from *Ygera* which lacked a septum, and also the 'ill-defined lobes of visceral field' (= bema) in *Ygera*. In fact, many populations of *Eoplectodonta* have specimens which lack a median septum, even in *E. duplicata* the type species, and similarly the bema is very variably developed and can even be entirely absent, particularly in small and young specimens. Thus we follow Cocks (1970) in not recognizing *Ygera* as a distinct genus. Hurst (1975) has described the ontogenetic development of the brachial valve septa and possible evolution of the lophophore in *Eoplectodonta transversalis*.

SPECIES ASSIGNED

Plectambonites trabeata var. *acuminata* Holtedahl, 1916: 79; pl. 14, figs 6–7 from 4ba Beds (M. Caradoc), Royal Palace, Oslo, Norway (revised Spjeldnaes, 1957: 96; pl. 3, figs 6–12).

Eoplectodonta acuminata Rozman, 1981 (*non* Holtedahl, 1916): 135; pl. 33, figs 1–11 from Bairimski Beds (Caradoc), south part of Mongolian Altai, W. Mongolia (certainly *Eoplectodonta* but different ornament from true *E. acuminata*).

Sowerbyella alternata Butts, 1942: 109; pl. 95, figs 22, 23 from Chambersburg Limestone (Caradoc), Strasburg, Shenandoah County, Virginia, U.S.A. (revised Cooper 1956: 808; pl. 184, figs 1–3; pl. 207, figs 2–25; pl. 208, figs 1–18; pl. 269, figs 23, 24).

Strophomena bidecorata Barrande, 1879: pl. 53, fig. 3 from Liteň Formation (Wenlock), hills between Loděnice and Bubovice, Czechoslovakia (revised Havlíček 1967: 61; pl. 7, figs 1–6).

Eoplectodonta budgei Sheehan, 1976: 726; pl. 4, figs 12–17 from Roberts Mountains Formation (U. Wenlock), Silver Island Mountains, Utah, USA.

Eoplectodonta californica Boucot, Johnson & Zhang, 1988: 110; pl. 3, figs 6–13 from Hidden Valley Dolomite (M. Wenlock), 2 km NW of Pyramid Peak, Funeral Mountains, California, USA.

Plectambonites sericea conspicua Reed, 1917: 882; pl. 15, figs 4–11 from Craighead Limestone (U. Caradoc), Craighead, Girvan, Scotland (revised Williams, 1962: 182; pl. 17, figs 32, 38, 39).

Plectodonta thraivensis var. *divergens* Reed, 1944: 216; pl. 3, figs 3, 3a from Craighead Limestone (U. Caradoc), Craighead, Girvan, Strathclyde (a junior synonym of *Eoplectodonta conspicua* – see Williams 1962: 182; Cocks 1978: 100).

Leptaena duplicata J. de C. Sowerby, 1839: 636; pl. 22, fig. 2 from Goleugoed Formation (L. Llandovery), Cefn Rhyddan, Llandovery, Wales, senior synonym of *Plectambonites transversalis* var. *mullochensis* Reed, 1917: 887; pl. 15, figs

41, 42; pl. 16, figs 1, 2 from Mulloch Hill Formation (L. Llandovery), Mulloch Hill, Girvan, Scotland; *Plectambonites transversalis* var. *tricostata* Reed, 1917: 889; pl. 16, figs 8–13 from Woodland Formation (L. Llandovery), Woodland Point, Girvan, Scotland; *Sowerbyella precursor* Jones, 1928: 437; pl. 23, figs 3–5 from U. Haverford Mudstone Formation (L. Llandovery), Haverfordwest, Dyfed, Wales; and *Sowerbyella superstes* Jones, 1928: 441; pl. 23, figs 10–12 from Gasworks Sandstone (L.–M. Llandovery), Haverfordwest, Dyfed, Wales (all revised Cocks 1970: 169; pl. 5, figs 1–12; pl. 6, figs 1–13; pl. 7, figs 1–11; pl. 8, figs 1–11 and Temple 1987: 60; pl. 6, figs 1–17).

Leptaena duvalii Davidson, 1847: 58; pl. 12, figs 20, 21 from Coalbrookdale Formation (U. Wenlock), Walsall, West Midlands, England, a senior synonym of *Sowerbyella transversalis* var. *lata* Jones, 1928: 450; pl. 24, fig. 2 from Buildwas Formation (L. Wenlock), Buildwas, Shropshire, England (all revised Cocks, 1970: 182; pl. 12, figs 14–16; pl. 13, figs 3, 7, 10)

Plectodonta exceptionis Rybnikova 1967: 189; pl. 19, figs 8–12 from M. Llandovery borehole in Latvia, USSR.

Plectodonta lenis Williams, in Whittington & Williams 1955: 417; pl. 39, figs 79–81 from Derfel Limestone (L. Caradoc), Trawsant, Gwynedd, Wales.

Eoplectodonta oscitanda Cocks, 1982: 769; pl. 81, figs 7, 9 from Langåra Limestone-Shale Formation (M.–U. Ashgill), Ringeriksveien, Sandvika, Norway.

Plectambonites schmidtii var. *precedens* Holtedahl, 1916: 81; pl. 15, figs 10–11 from 4b Beds (M.–U. Caradoc), Bratterud, Ringerike, Norway (revised Spjeldnaes 1957: 101; pl. 4, fig. 9; pl. 6, fig. 7).

Leptaena sericea var. *rhombica* M^cCoy, in Sedgwick & M^cCoy 1852: 239 (figured Jones 1928: pl. 22, fig. 1) from Crag Hill Beds (L. Ashgill), Horton-in-Ribblesdale, Cumbria, England (also revised Cocks 1982: 769; pl. 81, figs 5, 6).

Plectambonites sericea semirugata Reed, 1917: 884; pl. 15, figs 18–26 from L. Ardwell Mudstones (M. Caradoc), Ardmillan Braes, Girvan, Scotland (revised Williams 1962: 181; pl. 17, figs 24–27) and subspecies *plicata* Williams, 1962: 182; pl. 17, figs 28–31, 33–35 from Kiln Mudstones (U. Caradoc), Craighead, Girvan, Scotland.

Leptaena transversalis var. *sowerbyana* Barrande, 1848: 225; pl. 21, figs 19–20 from Liteň Formation (Wenlock), hills between Loděnice and Bubovice, Czechoslovakia (revised Havlíček 1967: 59; pl. 7, figs 12–24 as *Ygera sowerbyana*).

Anomites transversalis Wahlenberg, 1818: 64 from L. Visby Beds (U. Llandovery), Lundbjars, Gotland, Sweden (revised Cocks, 1970: 177; pl. 12, figs 1–13).

Plectambonites transversalis var. *penkillensis* Reed, 1917: 888; pl. 16, figs 3–7 from Wood Burn Formation (U. Llandovery), Bargany Pond Burn, Girvan, Scotland, senior synonym of *Sowerbyella millinensis* Jones, 1928: 444; pl. 23, figs 13–16 and subspecies *parabola* Jones, 1928: 446; pl. 23, figs 18–20 and *canastonensis* Jones, 1928: 447; pl. 23, figs 17, 21, 22 all from Millin Mudstone (U. Llandovery), near Haverfordwest, Dyfed, Wales (all revised Cocks, 1970: 172; pl. 9, figs 1–15; pl. 10, figs 1–12; pl. 11, figs 1–16).

Ygera ygerens Havlíček 1961: 450; pl. 1, figs 7–12 from U. Liteň Beds (Wenlock), Svaty Jan Hliník, Czechoslovakia.

Eoplectodonta sp. 1 of Cooper 1956: 813; pl. 192, figs 25–28 from Edinburg Formation (L. Caradoc), Wadesville, Winchester, Virginia, USA.

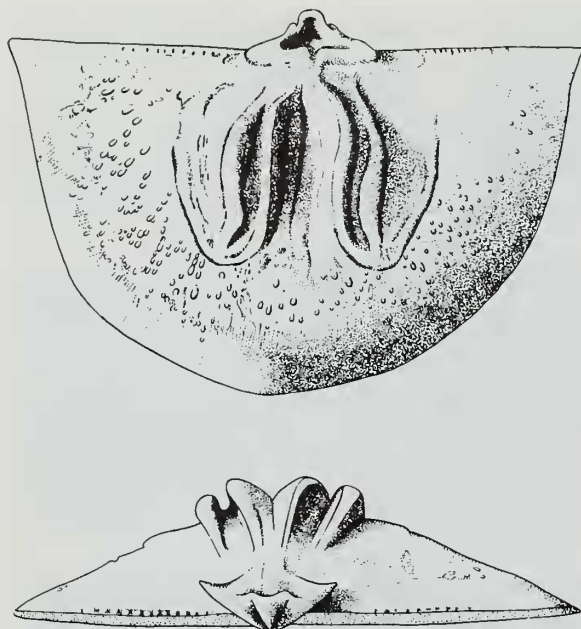


Fig. 137 *Eoplectodonta duvalii* (Davidson, 1847), from Slite Marl (Wenlock), Gotland, Sweden, posterior and downward views of a brachial valve interior (based on BB 31837), $\times 5$.

SPECIES QUESTIONABLY ASSIGNED

Leptaena transversalis var. *alabamensis* Foerste, 1890: 293; pl. 5, fig. 9 from Clinton Group (U. Llandovery), Collinsville, Alabama, USA (no interiors figured).

Plectambonites delicatula Butts, 1926: 116; pl. 26, figs 20–21 from Little Oak Limestone (U. Llandovery–L. Caradoc), Pelham, Alabama, USA (no interiors figured).

Sowerbyella elegans Poulsen, 1943: 15; pl. 2, fig. 4 from Offley Island Formation (Wenlock–Ludlow), Cape Bryan, north Greenland (no brachial interior illustrated).

Strophomena elegantula Hall, 1843: 72; fig. 17.1 from Clinton Group (U. Llandovery), Rochester, New York, USA (no interiors figured).

Leptaena transversalis var. *elegantula* Foerste, 1890: 293; pl. 6, fig. 6 from Clinton Group (U. Llandovery), Hanover, Indiana, USA (no interiors figured).

Eoplectodonta foerstei Cooper, 1956: 811; pl. 209, figs 1–3 from Wells Formation (L. Caradoc), SW of Cumberland City, Tennessee, USA (no interiors figured).

Eoplectodonta (Eoplectodonta) semirugata paucicostellata Rozman, 1978: 92; pl. 15, figs 1–6 from Obikalon Beds (U. Caradoc), Shakhriomon, Tian-Shan, USSR (denticles not preserved).

Leptaena transversalis var. *prolongata* Foerste, 1890: 293; pl. 5, fig. 13 from Clinton Group (U. Llandovery), Wildwood Station, Georgia, USA (no interiors figured).

Eoplectodonta? pumila Lopushinskaya 1976: 36; pl. 3, figs 3–8 from *Dalmanella neocrassa* Beds (U. Llandovery), River Sukhaya Tunguska, N. Siberia USSR (no interiors known).

Plectambonites tenera Shaler, 1865: 65, not illustrated, but said by Twenhofel (1928: 192) to be a synonym of *E. transversalis* and come from Gun River and Jupiter Formations (M.–U. Llandovery), Anticosti Island, Quebec, Canada (no interiors known).

Eoplectodonta transversalis sibirica Lopushinskaya, 1976: 37; pl. 3, figs 1–2 from *Dalmanella neocrassa* Beds (U. Lland-

overy), River Sukhaya, N. Siberia, USSR (no interiors known).

SPECIES REJECTED

Eoplectodonta? dubia Cooper 1956: 810; pl. 207, fig. 1; pl. 209, figs 8–13 from Botetourt Formation (L. Caradoc), Brownsburg, Virginia, USA (no hinge denticles, transferred to *Sowerbyella*).

Eoplectodonta karina Spjeldnaes, 1957: 100; pl. 3, fig. 5 from 4ba Beds, southern end of Nakholmen, Oslo, Norway (to *Anisopleurella*).

Eoplectodonta (Eoplectodonta) killeyensis Reed, 1952: 51; pl. 2, figs 8, 9 from Killey Bridge Formation (L. Ashgill), Pomeroy, Co. Tyrone, Northern Ireland (revised Mitchell 1977: 81 as a junior synonym of *Sowerbyella thraivensis* Reed).

EOPLECTODONTA (KOZLOWSKITES) Havlíček, 1952

1952 *Kozlowskites* Havlíček: 406

1965 *Eoplectodonta (Kozlowskites)* Williams: H381

1967 *Kozlowskites* Havlíček: 56

TYPE SPECIES. *Strophomena nuntia* Barrande, 1879.

DIAGNOSIS. Like *Eoplectodonta* but ventral muscle scars not united centrally. Pedicle valve pallial markings simple and subparallel.

REMARKS. We agree with Havlíček (1967: 56) that the denticles in *Kozlowskites* can occupy only a very short distance of the central parts of the hinge line. We follow Williams (1965: H381) in regarding *Kozlowskites* as a subgenus of *Eoplectodonta*.

SPECIES ASSIGNED

Spirifer? ichnusae Vinassa, 1927: 491; pl. 4, fig. 35 from Portixeddu Formation (U. Caradoc), Portixeddu, Sardinia, Italy (revised Havlíček *et al.* 1987: 307; pl. 8, figs 23, 24; pl. 9, figs 1, 2).

Strophomena nuntia Barrande, 1879: pl. 49, fig. 3 from Králův Dvůr Formation (M. Ashgill), Králův Dvůr, Bohemia, Czechoslovakia (revised Havlíček 1967: 56; pl. 6, figs 10–18).

Eoplectodonta (Kozlowskites) ragnari Sheehan, 1973: 63; pl. 2, figs 3–8 from Jerrestad Mudstone (L. Ashgill), Fågelsång, Scania, Sweden.

Kozlowskites yichangensis Chang, 1983: 479; pl. 1, figs 16–23 from Miaopo Formation (L. Caradoc), Huanghuachang, Yichang County, Hubei, China.

EOPLECTODONTA (YGERODISCUS) Havlíček 1967

1967 *Ygerodiscus* Havlíček: 62

1970 *Ygerodiscus* Cocks: 184

1970 *Eoplectodonta* Temple: 43 *pars*

1974 *Ygerodiscus* Bassett: 90

TYPE SPECIES. *Leptaena transversalis* var. *undulata* Salter, 1848.

DIAGNOSIS. Like *Eoplectodonta (Eoplectodonta)* but with distinctive shell undulations.

REMARKS. Since Havlíček established this genus there has been discussion on the proper systematic weighting to be

given to the distinctive undulations, for example Temple (1970: 43) considered that those in the type species which he was revising merited no more than subspecific recognition. However, we follow Cocks (1970: 184) in treating *Eoplectodonta* and *Ygerodiscus* as distinct because of the presence of the two forms in the same bedding plane at Meifod without intermediates, but consider the differences to be of sub-generic rather than generic rank.

SPECIES ASSIGNED

Leptaena segmentum var. *cornuta* Davidson, 1883: 166; pl. 12, figs 1–3 from Coalbrookdale Formation (Wenlock), Coalbrookdale, Shropshire, England (revised Cocks 1970: 188; pl. 13, figs 11, 12; pl. 14, figs 1, 2 and Bassett 1974: 90; pl. 22, figs 7–10).

Ygerodiscus novemcostatus Havlíček, 1967: 62; pl. 9, figs 21, 22 from U. Liteň Formation (Wenlock), Lističe, Beroun, Czechoslovakia.

Plectodonta propinqua Rybníková, 1967: 191; pl. 19, figs 3–7 from L. Llandovery rocks in boreholes, Latvia, USSR.

Plectambonites striatacostatus Twenhofel, 1928: 191; pl. 16, figs 16, 17 from L. Jupiter Formation (U. Llandovery), Jupiter River, Anticosti Island, Canada.

Leptaena transversalis var. *undulata* Salter, in Phillips & Salter 1848: 372; from V₂C Beds (L. Llandovery), Mathyrafal, Meifod, Wales, a senior synonym of *Sowerbyella undulata* var. *maccoyi* Jones, 1928: 457; pl. 24, fig. 7 from the same horizon and locality, *Sowerbyella plicata* Jones, 1928: 459; pl. 24, figs 10, 11 from Rosemarket Beds (M. Llandovery), Bullford, Dyfed, Wales, and *Sowerbyella compressa* Jones, 1928: 460; pl. 24, figs 12, 13 from the same horizon and locality (all revised Cocks 1970: 185; pl. 14, figs 3–12; pl. 15, figs 1–12).

SPECIES QUESTIONABLY ASSIGNED

Plectambonites tennesseensis Foerste, 1903: 708 from Waldron Formation (Wenlock), Clifton, Tennessee, USA (no interiors or exteriors figured).

GUNNINGBLANDELLA Percival, 1979

1979 *Gunningblandella* Percival: 111

TYPE SPECIES. *Gunningblandella resupinata* Percival, 1979.

DIAGNOSIS. Like *Sowerbyella* but resupinate in shell profile. Hinge line not denticulate.

REMARKS. This is the only resupinate genus within the Sowerbyellidae and is so far definitely known only from the type species in the Caradoc of Australia.

SPECIES ASSIGNED

Gunningblandella resupinata Percival, 1979: 111, fig. 9: 1–25, from Goonumbla Volcanics (U. Caradoc), Gunningbland, New South Wales, Australia.

SPECIES QUESTIONABLY ASSIGNED

Stropheodonta katuglåsensis Reed, 1932a: 136; pl. 21, figs 1–6, ?fig. 13 from Hølandet Formation (Caradoc), Katuglåsén, Trondheim, Norway (one shell is certainly resupinate, but whether or not all the shells figured by Reed belong to one species, and whether or not the 'minute denticulations' described but not figured by Reed are real, all remain doubtful).

PLECTODONTA (PLECTODONTA) Kozłowski, 1929

Figs 153–157

1929 *Plectodonta* Kozłowski: 112

1954 *Plectodonta* Nikiforova: 79

1965 *Plectodonta* Williams: H381 pars

TYPE SPECIES. *Plectodonta mariae* Kozłowski, 1929.

DIAGNOSIS. Hinge line denticulate. Bema weak or absent. Platform absent. Like *Eoplectodonta* except with strong deltidium, less incurved, more quadrate and less alate valve extremities, and with coarse papillae on the brachial valve interior.

REMARKS. The distinctive deltidium has been illustrated by Kozłowski (1929: fig. 36A), Cocks (1970: fig. 3) and Nikiforova *et al.* (1985: pl. 3, fig. 6b). Although the form and presence of coarse papillae inside the brachial valve is not usually regarded by us as a good generic character within the Plectambonitacea, nevertheless their universal presence within the *Plectodonta* group is noteworthy.

SPECIES ASSIGNED

Chonetes bipartita Chapman, 1913: 104; pl. 10, figs 8–10 from Yering Siltstones (Pridoli–Lochkov), Ruddock's Quarry, near Lilydale, Victoria, Australia.

Stropheodonta davidi Mitchell, 1923: 470; pl. 41, figs 19–21 from Upper Trilobite Bed of Hume Series (Pridoli–Lochkov), Bowring railway station, New South Wales, Australia, and *Stropheodonta striato-costata* Mitchell, 1923: 472; pl. 42, figs 29, 30 and *Stropheodonta striato-punctata* Mitchell, 1923: 472; pl. 42, fig. 31, both from the same horizon and locality and regarded as synonyms of *davidi* by Brown (1949: 199). Savage (1974:27) regards them all as junior synonyms of *Plectodonta bipartita* (Chapman).

Plectambonites minor var. *digitata* Wolburg, 1933: 53; pl. 2, fig. 6 from Robecke Shale (M. Devonian), Winkhausen, Girkhausen, Germany (as revised by Solle 1938: 268, fig. 5).

Plectodonta mariae Kozłowski, 1929: 114; pl. 3, figs 30–32 from Mitkov Beds, Borschchov Horizon (Lochkov), Podolia, Ukraine, USSR (formerly Poland).

Strophomena mimica Barrande, 1879; pl. 107, fig. 9 from Lochkov Limestones (Lochkov), Lochkov, Czechoslovakia (revised Havlíček 1967: 64; pl. 8, figs 6, 7, 10).

Plectodonta pacifica Hamada, 1969: 4; pl. 1, figs 5–7; pl. 2, fig. 3 from beds of L.–M. Devonian age, Kampong Pahil, south of Kroh, Perak, Malaysia.

Plectodonta petila Amsden, 1958: 93; pl. 13, figs 8–17 from Haragan Formation (L. Devonian), White Mound, Murray County, Oklahoma, USA.

Sowerbyella ? *plebia* Talent, 1965: 23; pl. 5, figs 6, 7 from McIvor Formation (Pridoli?), Redcastle, Victoria, Australia.

Plectodonta sanglangensis Xian, 1978: 262; pl. 97, figs 2–3 from Nabiao Formation (Eifelian), Sanglang, Ludian County, S. Guizhou Province, China.

Plectodonta thuringica Schmidt, 1939: 80; pl. 3, figs 1, 2 from Ludlow–Pridoli beds, Ebersdorf–Katzenwisch, Thuringia, Germany.

SPECIES QUESTIONABLY ASSIGNED

Plectodonta minor var. *alatifformis* Schmidt, 1939: 83; pl. 4, fig. 8 from Tentaculitenkalk (L. Devonian), Schleizer Stadtwald, Thuringia, Germany.

Plectodonta biplexa Xu, 1979: 370; pl. 2, figs 14–16 from

Tangxiang Formation (Eifelian), Luofu of Nandan, Guanxi Province, China (no interiors illustrated).

Plectodonta burtonae Hamada, 1969: 5; pl. 1, figs 8, 9 from beds of L.-M. Devonian age, Kampong Pahil, south of Kroh, Perak, Malaysia (no brachial interiors figures; might be chonetacean).

Sowerbyella (Plectodonta) hopfi Volk, 1939: 388; fig. 1 from Lower Middle Devonian Beds, Pfeiffersberg, Steinach, Thuringia, Germany (poorly preserved specimens, but Jahnke (1971: 51) considers the species to be a junior synonym of *Plectodonta (Dalejodiscus) minor*).

Plectodonta loilemensis Reed, 1936: 113; pl. 4, figs 16–20 from Loilem Formation (Ludlow?), Loilem, Southern Shan States, Burma (no brachial interiors figured).

SPECIES REJECTED

Plectodonta aknistensis Rybnikova 1967: 188; pl. 19, figs 1, 2 from L. Ludlow borehole in Latvia, USSR (assigned here to *Jonesea*).

Plectodonta thraivensis var. *divergens* Reed, 1944: 216; pl. 3, figs 3, 3a from Craighead Limestone (U. Caradoc), Craighead, Girvan, Strathclyde, Scotland (transferred to *Eoplectodonta (Eoplectodonta)*).

Plectodonta exceptionis Rybnikova, 1967: 189; pl. 19, figs 8–12 from M. Llandovery borehole in Latvia, USSR (assigned here to *Eoplectodonta (Eoplectodonta)*).

Plectodonta propinqua Rybnikova, 1967: 191; pl. 19, figs 3–7 from L. Llandovery borehole in Latvia, USSR (assigned here to *Eoplectodonta (Ygerodiscus)*).

Plectodonta shiqianensis Xian, 1978: 262; pl. 96, fig. 16 from Xiushan Formation (U. Llandovery), Raochaguan, Shiqian County, NE Guizhou, China (to *Mesopholidostrophia*).

Plectodonta sp. of Harper 1973: 51; pl. 16, figs 1, 2 from French River Formation (L. Wenlock), Cobequid Mountains, Nova Scotia, Canada (certainly *Eoplectodonta*).

PLECTODONTA (DALEJODISCUS) Havlíček, 1961

- 1961 *Dalejodiscus* Havlíček: 449
 1965 *Plectodonta* Williams: H381 *pars*
 1967 *Dalejodiscus* Havlíček: 65
 1971 *Plectodonta (Dalejodiscus)* Jahnke: 51

TYPE SPECIES. *Strophomena comitans* Barrande, 1879.

DIAGNOSIS. Like *Plectodonta (Plectodonta)*, but with elevated and radially striated bema.

REMARKS. Havlíček's (1967) illustrations of the two Bohemian species clearly show the internal characteristics of the brachial valve and can be compared with the interior of *Plectodonta mariae*, e.g. the specimen figured by Williams (1965: fig. 243). Solle's illustrations of *P. wolburgi* provide the link between *Plectodonta* and *Dalejodiscus*, where it can be seen that, although the bema is slightly elevated anteriorly and also has a few striations, nevertheless the general morphology is close to that of *Plectodonta mariae*.

SPECIES ASSIGNED

Strophomena comitans Barrande, 1879: pl. 56, figs 4–6, 21–23, 30–32, 42, 43, 46–48 from Daleje shales (Eifelian), Praha-Hlubocepy, Czechoslovakia (revised Havlíček 1967: 67; pl. 7, figs 8–11).

Leptaena minor Roemer, 1850: 12; pl. 3, fig 1 from Wissenbach Shale (Eifelian), Ziegenberger Teich, NE Buntentock,

Germany (revised Jahnke 1971: 51; pl. 2, figs 1–3; Jahnke also considered *P. comitans*, *P. wolburgi* and *P. hopfi* to be junior synonyms of *P. minor*).

Plectodonta subcomitans Havlíček 1956: 554; pl. 8, figs 14–18 from Dvorce-Prokop limestones (Pragian), Praha-Branik, Czechoslovakia (revised Havlíček 1967: 65; pl. 8, figs 8, 9, 11–16, but not *D. subcomitans* of Havlíček 1977; pl. 1, fig. 6, from Zlichovian, Stary Rozmital, Czechoslovakia, here assigned to *Plectodonta (Plectodonta)*).

Sowerbyella (Plectodonta) wolburgi Solle, 1938: 271, figs 6–10 from Lower Devonian of Hilgenfeld, Kellerwald, Germany.

SPECIES QUESTIONABLY ASSIGNED

Dalejodiscus? sp. of Gratsianova 1967: 34; pl. 2, fig. 1 from Yarkushinski Beds (L. Devonian), Gornoi Altai, Central USSR (no interiors known).

PLECTODONTA (PLECTODONTELLA) Havlíček, 1953

- 1953 *Plectodontella* Havlíček: 8
 1965 *Plectodontella* Williams: H381 *pars (non Ygera)*
 1967 *Plectodontella* Havlíček: 69

TYPE SPECIES. *Plectodontella redunca* Havlíček, 1953.

DIAGNOSIS. Like *Plectodonta (Plectodonta)* but with strong raised bema. Weak platform present.

SPECIES ASSIGNED

Plectodontella redunca Havlíček, 1953: 9; pl. 1, fig. 4 from Třebotov Limestones (L. Eifelian), Holyně, Prague, Czechoslovakia (revised Havlíček 1967: 69; pl. 9, figs 5, 8, 9, 12).

SOWERBYELLA (SOWERBYELLA) Jones, 1928

Figs 138–148

- 1928 *Sowerbyella* Jones: 384
 1930 *Sowerbyella* Öpik: 144 *pars*
 1959 *Sowerbyella (Viruella)* Rõõmusoks: 14
 1965 *Sowerbyella* Williams: H378
 1981 *Sowerbyella (Sowerbyella)* Rozman: 133
 1984 *Sowerbyella* Klenina: 77

TYPE SPECIES. *Leptaena sericea* J. de C. Sowerby, 1839. The type species of *Viruella* is *Sowerbyella liliifera* Öpik, 1930.

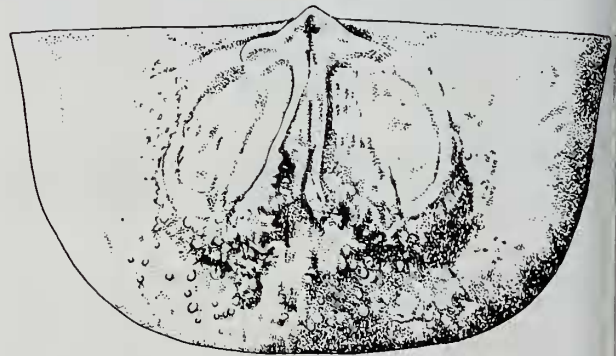


Fig. 138 *Sowerbyella (Sowerbyella) sericea* (J. de C. Sowerby, 1839), from Horderley Sandstone (L. Caradoc), Shropshire, England, brachial valve interior (based on BC 6051–3), $\times 6$.

DIAGNOSIS. Bema variable, sometimes absent. No denticles on hinge line. Median septum in brachial valve variably developed, usually absent. Like *Anisopleurella* but with prominent pair of central side septa, which sometimes form the edge of the bema and are sometimes developed above it.

REMARKS. Rõõmusoks (1959) separated a subgenus *Viruella* based on ornamentation (like *Eoplectodonta*), the presence of a median septum in the brachial valve, and a raised muscle platform in the brachial valve. However, those three characters show great variation, and in fact all are present in the type species of *Sowerbyella*, *S. sericea*, apart from the ornamental difference, which we regard as of specific, not generic importance. We illustrate topotype specimens of both nominal genera.

SPECIES ASSIGNED

Sowerbyella (Viruella) acculica Misius, 1986: 154; pl. 14, figs 14–32 from Tabilgat Formation (U. Llandeilo), River Tabilgat, Moldo-Too, N. Khirgizia, USSR.

Sowerbyella aequicostellata Cooper, 1956: 774; pl. 199, figs 9–17 from Edinburg Formation (L. Caradoc), Strasburg Junction, Virginia, USA.

Sowerbyella (Sowerbyella) akdombakensis Klenina, in Klenina *et al.* 1984: 82; pl. 7, figs 12, 15, 17, 19, 20, 22; pl. 9, figs 2, 3 from Akdombak Formation (M. Ashgill), Akdombak Hill, Chinghiz Mountains, Kazakhstan, USSR.

Sowerbyella angulata Cooper, 1956: 776; pl. 206, figs 1–7 from Hermitage Formation (L. Caradoc), Birmingham, Alabama, USA.

Sowerbyella antiqua Jones, 1928: 419; pl. 21, figs 7–11 from Llandeilo beds, Llandeilo, Dyfed, Wales (revised Lockley & Williams 1981: 58; figs 196–212), including its junior synonym *Sowerbyella antiqua llandeiloensis* Williams, 1949: 234; pl. 11, figs 12–14 from L. Llandeilo beds, Dynevor, Llandeilo, Dyfed, Wales.

Sowerbyella sericea askerensis Spjeldnaes, 1957: 92; pl. 6, fig. 5 from 4bδ Beds (M. Caradoc), Hvalstad, Asker, Norway.

Sowerbyella (Viruella) bystrovi Nikanorova 1976: 117; figs 1b–k from Tallinn Horizon (Llandeilo–L. Caradoc), Tolbykhin, River Yaroslavlyar, Moscow synecise, USSR.

Sowerbyella cava Cooper, 1956: 777; pl. 203, figs 21–43 from Martinsburg Formation (L. Caradoc), Green Mount Church, Virginia, USA.

Sowerbyella compacta Cooper 1956: 778; pl. 196, figs 51–59; pl. 197, figs 11–24; pl. 200, figs 1–6; pl. 202, figs 1–8 from Benbolt Formation (L. Caradoc), Rye Cove, Clinchport, Virginia, USA.

Plectambonites curdsvillensis Foerste, 1912: 122; pl. 10, figs 15a, b from Curdsville Formation (M. Caradoc), Glenn Creek Station, Woodford County, Kentucky, USA (revised Cooper 1956: 780; pl. 201, figs 1–13, Howe 1979: 1; pl. 1, figs 6–16, and Rice 1987: 156; pl. 3, fig 1).

Eoplectodonta? dubia Cooper, 1956: 810; pl. 207, fig. 1; pl. 209, figs 8–13 from Botetourt Formation (L. Caradoc), Brownsburg, Virginia, USA.

Sowerbyella elusa Williams, 1962: 181; pl. 17, figs 20–23, from Craighead Limestone (U. Caradoc), Craighead, Girvan, Scotland.

Sowerbyella eximia Cooper, 1956: 781; pl. 204, figs 13–33; pl. 205, figs 7, 8 from Martinsburg Formation (L. Caradoc), Green Mount Church, Virginia, USA.

Sowerbyella fallax Jones, 1928: 493 (illustrated Reed 1917: pl. 13, fig. 14) from Craighead Limestone (U. Caradoc), Craighead, Girvan, Scotland.

Sowerbyella (Soweryella) forumi Rõõmusoks, 1959: 30; pl. 5, figs 1–9 from Keila Horizon (M.–U. Caradoc), Rakvere, Estonia, USSR.

Sowerbyella fupingensis Fu, 1982: 118; pl. 35, figs 4–6 from Beiguoshan Formation (U. Caradoc–L. Ashgill), Hongshui, Fuping County, Shaanxi Province, China.

Sowerbyella grierensis Howe, 1979: 3; pl. 1, figs 1–5 from Grier Limestone Member of Lexington Formation (M. Caradoc), Grier, Kentucky, USA.

Sowerbyella sericea hadelandica Spjeldnaes, 1957: 93; pl. 4, figs 1, 7 from Lower Cyclocrinus Beds (Caradoc), between Jonsrud and Stensrud, Hadeland, Norway.

Sowerbyella hainanensis Xu & Su, 1979: 106 from Middle Ordovician beds, Yaxian, Hainan Island, China.

Sowerbyella indistincta Cooper, 1956: 782; pl. 202, figs 24–26 from Bromide Formation (U. Llandeilo), NE of Springer, Carter County, Oklahoma, USA.

Sowerbyella (Viruella) insueta Klenina, in Klenina *et al.* 1984: 84; pl. 8, figs 8–10 from Taldiboiskaya Formation (L. Ashgill), Taldiboy River, Chinghiz Mountains, Kazakhstan, USSR.

Sowerbyella intricata Nikiforova, 1978: 108; pl. 19, figs 12–20 from Archalyk Beds (Ashgill), Shakhriomon, Tian Shan, USSR.

Plectodonta (Eoplectodonta) killeyensis Reed, 1952: 51; pl. 2, figs 8, 9 from Killey bridge Formation (L. Ashgill), Pomeroy, Co. Tyrone, Northern Ireland (revised Mitchell 1977: 81 and put in the synonymy of *Sowerbyella thraivensis* Reed).

Sowerbyella lanxiensis Liang, in Liu *et al.* 1983: 276; pl. 99, figs 1–3 from Changwu Formation (M. Ashgill), Zhuganshan, Lanxi County, Zhejiang Province, SE China.

Sowerbyella lebanonensis Bassler, 1935: 406 from Lebanon Formation (L.–M. Caradoc), Shelbyville, Bedford County, Tennessee, USA (revised Cooper 1956: 782; pl. 201, figs 14–25).

Sowerbyella (Sowerbyella) lepta Percival, 1979: 108, figs 3B.4–7, 8 from Goonumbla Volcanics (L. Caradoc), Gunningbland, New South Wales, Australia.

Sowerbyella liliifera Öpik, 1930: 148; pl. 8, fig. 112; pl. 9, fig. 119; pl. 21, figs 262–4 from Kukruse Formation, (L. Caradoc), Kohtla, Estonia, USSR and subspecies *milis* Öpik 1930: 151; pl. 9, figs 115, 120 from same horizon and locality, and the subspecies *tegula* Öpik, 1930: 151; pl. 8, fig. 113; pl. 9, fig. 117 and *triangulum* Öpik 1930: 153; pl. 9, fig. 118, both from Idavere Formation (L. Caradoc), Kohtla, Estonia, USSR (all revised Rõõmusoks, 1959: 18; pl. 2, figs 1–13).

Sowerbyella limata Öpik, 1930: 163; pl. 9, fig. 128 from Kukruse Formation (L. Caradoc), Kohtla, Estonia, USSR.

Sowerbyella (Viruella) minima Rõõmusoks, 1959: 22; pl. 3, figs 1–6 from Kukruse Horizon (L. Caradoc), Lasnamagi, Estonia, USSR.

Leptaena minnesotensis Sardeson, 1892: 329; pl. 4, figs 24, 25 from Decorah Shale (M. Caradoc), Minnesota, USA (revised Rice 1987: 157; pl. 3, fig. 2).

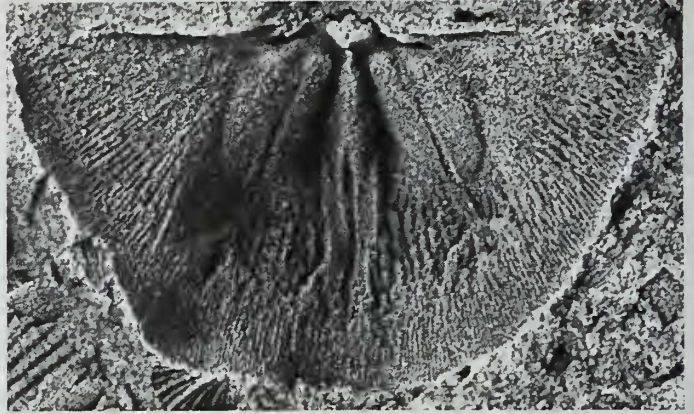
Sowerbyella monilifera Cooper, 1956: 785; pl. 199, figs 1–8; pl. 206, figs 16–28 from Decorah Formation (L.–M. Caradoc), Ellsworth, Wisconsin, USA.

Sowerbyella multipartita Williams, in Cocks 1978: 98, nom. nov. pro *S. multiseptata* Williams, 1974: 132; pl. 23, figs 14–19; pl. 24, figs 1, 3 from Spy Wood Grit (L. Caradoc), 1 km NNE of Rorrington, Shropshire, England.

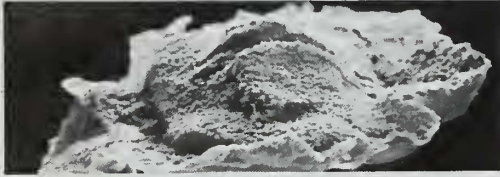
Sowerbyella musculosa Williams, 1963: 433; pl. 11, figs 18–27 from Allt Ddu Group (L. Caradoc), Bala, Gwynedd, Wales.



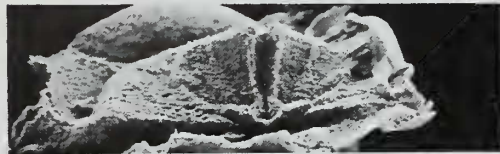
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139b



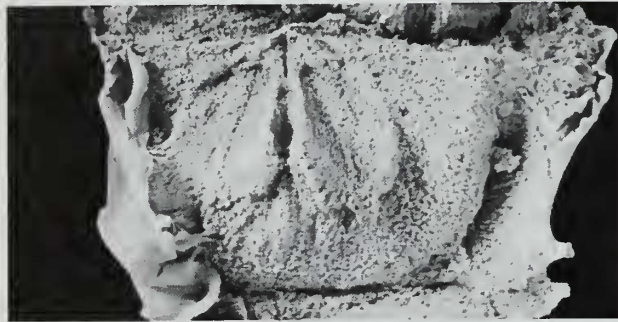
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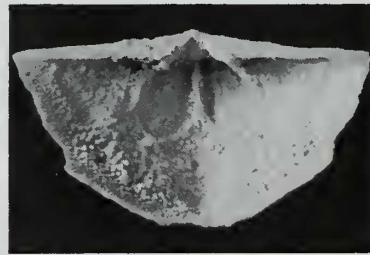
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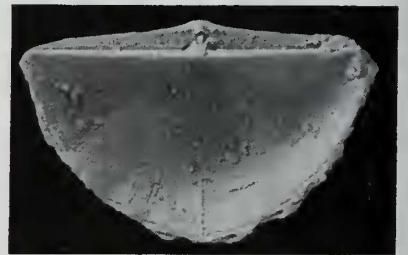
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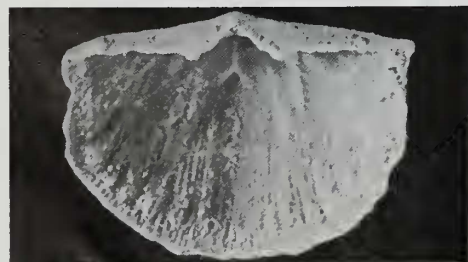
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148a



148b

- Chonetoidea (Aegiria) nacta* Reed, 1952: 53; pl. 2, fig. 13 from Killey Bridge Formation (L. Ashgill), Pomeroy, Co. Tyrone, Northern Ireland (revised Mitchell 1977: 81 and put in the synonymy of *Sowerbyella thraivensis*).
- Sowerbyella nasuta* Cooper, 1956: 787; pl. 199, figs 18–34; pl. 215, figs 1–4 from Chatham Hill Formation (L. Caradoc), Walker Mountain, Chatham Hill, Virginia, USA.
- Sowerbyella (Sowerbyella) nativa* Klenina, in Klenina *et al.* 1984: 78; pl. 6, figs 4–6, 8, 9; pl. 7, fig. 11 from Abaevskaya Formation (Llanvirn–Llandeilo), SE Ordatas Hill, NE Pre-Chinghiz, Kazakhstan, USSR.
- Sowerbyella (Sowerbyella) oepiki* Rõõmusoks, 1959: 32; pl. 6, figs 1–9 from Keila Horizon (M.–U. Caradoc), Lekhtmetša-Saky, Estonia, USSR.
- Viruella orientalis* Su, 1980: 272; pl. 115, figs 5–9 from Guanniaohe Formation (M. Ordovician), Less Hinggan, Heilongjiang Province, NE China.
- Sowerbyella papiliunculus* Borissiak, 1972: 183; pl. 49, figs 4–7 from Amsassia Beds (U. Caradoc), Kulunbulak River, Tarbagatau Mountains, E. Kazakhstan, USSR.
- Sowerbyella parva* Cooper, 1956: 789; pl. 202, figs 9–15 from Ward Cove Formation (L. Caradoc), N. of Rye Cove, Clinchport, Tennessee, USA.
- Sowerbyella perplexa* Cooper, 1956: 790; pl. 196, figs 30–44 from Chatham Hill Formation (L. Caradoc), Sharon Springs, Burkes Garden, Virginia, USA.
- Plectambonites punctostriatus* Mather, 1917: 38; pl. 1, figs 15–17 from Rockland Formation (M. Caradoc), Wolfe Island, Lake Ontario, Canada (revised Cooper 1956: 792; pl. 205, figs 9–25; pl. 206, figs 14, 15 and put into the synonymy of *Sowerbyella curdsvillensis* by Rice 1987: 156).
- Sowerbyella (Sowerbyella) raegaverensis* Rõõmusoks, 1959: 36; pl. 8, figs 1–8 from Rakvere Horizon (L. Ashgill), Ragavere, Estonia, USSR.
- Sowerbyella ringsakerensis* Spjeldnaes, 1957: 94; pl. 6, figs 1–4 from Coelosphaeridium Beds (M. Caradoc), between Tørud and Bratberg, Ringsaker, Norway.
- Plectambonites rugosa* Meek, 1873: 72; pl. 5, figs 3f–h from L. Edenian Strata (U. Caradoc), Ohio River, Cincinnati, Ohio, USA (revised Howe 1972: 444; pl. 1, figs 4–7 and Howe, 1979: 3; pl. 1, figs 17–20).
- Sowerbyella rukavishnikovae* Popov, 1980b: 151; pl. 2, figs 1–4 from Anderkenskaya Horizon (U. Llandeilo–L. Caradoc), Anderken-Ashkov river, Chu-Ili Mountains, Kazakhstan, USSR.
- Sowerbyella semiluna* Öpik, 1930: 155; pl. 9, figs 123–6 from Idavere Formation (L. Caradoc), Kohtla, Estonia, USSR.
- Leptaena sericea* J. de C. Sowerby, 1839: 636; pl. 19, fig. 1 from Horderley Sandstone (L. Caradoc), Whittingslow, Shropshire, England (revised Williams 1963: 430; pl. 11, figs 1–9) and subspecies *brynensis* Whittington, 1938: 253; pl. 11, figs 6–9 from L. Caradoc beds, Powys, Wales and *permixta* Williams, 1963: 434; pl. 11, figs 10–17 from Nant-Hir Group (L. Caradoc), Bala, Gwynedd.
- Sowerbyella sericea jugata* Ruedemann, 1912: 92; pl. 4, fig. 7 from Snake Hill Shale (U. Caradoc), Snake Hill, Mohawk Valley, New York, USA.
- Sowerbyella sericea tchernyshevi* Rozman, 1977: 92; pl. 6, figs 1–3 from *P. linearis* Zone (U. Caradoc), River Bairimgol, NW Mongolia.
- Sowerbyella sladensis* Jones, 1928: 421; pl. 21, figs 14–17 from Slade and Redhill Mudstone Formation (M. Ashgill), Llan Mill, Dyfed, Wales, and subspecies *simulans* Jones, 1928: 423; pl. 21, figs 18–20 from same formation at Narberth, Dyfed, Wales (comments in Cocks 1978: 98).
- Sowerbyella socialis* Cooper, 1956: 794; pl. 198, figs 23–44; pl. 205, figs 1–6 from Wardell Formation (L. Caradoc), Rye Cove, Clinchport, Tennessee, USA (and subspecies *crassa* Cooper, 1956: 796; pl. 200, figs 7–14, from same horizon and locality).
- Sowerbyella soudleyensis* Jones, 1928: 417; pl. 21, figs 5, 6 from Horderley Sandstone (L. Caradoc), Whittingslow, Shropshire, England (revised Williams 1963: 432; pl. 12, figs 1–8).
- Plectambonites subcarinatus* Ulrich, in Butts 1926: 126; pl. 31, figs 9–15 from Chickamauga Limestone (L.–M. Caradoc), Cedar Mountain, Argo, Alabama, USA (revised Cooper 1956: 797; pl. 200, figs 15–18).
- Sowerbyella (Sowerbyella) tamdysvensis* Misius, 1986: 150; pl. 15, figs 1–18; pl. 16, figs 1–6 from Ichkebash Formation (M. Caradoc), Djebagl Mountain, N. Khirgizia, USSR.
- Sowerbyella (Sowerbyella) tenera* Rõõmusoks, 1959: 34; pl. 7, figs 1–11 from Oandu Horizon (U. Caradoc), Rakvere, Estonia, USSR.
- Plectambonites sericea* var. *thraivensis* Reed, 1917: 885; pl. 15, figs 27–32 from Upper Drummuck Group (M. Ashgill), Thraive Glen, Girvan, Scotland (revised Mitchell 1977: 81; pl. 16, figs 9–22).
- Sowerbyella (Sowerbyella) triviva* Rõõmusoks, 1959: 27; pl. 4, figs 5–12 from Keila Horizon (M.–U. Caradoc), Kaikula, Estonia, USSR.
- Sowerbyella (Viruella) uhakuana* Rõõmusoks, 1959: 16; pl. 1, figs 3–12 from Uhaku Horizon (U. Llandeilo), Kivili River, Estonia, USSR.
- Sowerbyella variabilis* Cooper, 1956: 798; pl. 197, figs 35–43; pl. 202, figs 27–40 from Bromide Formation (U. Llandeilo), Hickory Creek, Criner Hills, Oklahoma, USA.
- Sowerbyella varicostellata* Cooper, 1956: 799; pl. 196, figs 1–8 from M. Arline Formation (U. Llandeilo), Friendsville, Concord, Tennessee, USA.
- Sowerbyella verecunda* Nikitin & Popov, 1983: 239; pl. 3, figs 7, 8, 10, 12, 16, 17 from Andriushenkaya Formation (M. Ordovician), Ishim River, Central Kazakhstan, USSR.

Figs 139–141 *Sowerbyella (Sowerbyella) sericea* (J. de C. Sowerby), from Horderley Sandstone Formation (L. Caradoc). Figs 139, 141 from quarry by New House, Onny Valley, Shropshire, England, Fig. 140 from Cheney Longville Lane, Onny Valley, Shropshire; Fig. 139, downwards and oblique lateral views of latex cast of a brachial valve interior, BC 6052, $\times 5$ and $\times 4$; Fig. 140, natural internal mould of brachial valve, BC 7303, $\times 5$; Fig. 141, posterior, oblique lateral and downwards views of latex cast of a brachial valve, BC 6051, a, b, $\times 4$, c, $\times 5$.

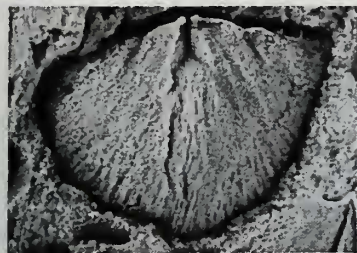
Fig. 142 *Sowerbyella (Sowerbyella) sp.*, natural internal mould of a brachial valve from Lower Miapo Formation (Llandeilo), Huanghuachang, Yichang County, Hubei Province, China, BC 3307, $\times 2.5$.

Fig. 143 *Sowerbyella (Sowerbyella) fallax* Jones, 1928, holotype by monotypy, a brachial valve, the original of Reed 1917: pl. 13, fig. 14, from Craighead Limestone (U. Caradoc), Craighead Quarry, Girvan, Strathclyde, Scotland, B 73436, $\times 3$.

Figs 144–148 *Sowerbyella (Sowerbyella) liliifera* Öpik, 1930, topotypes from Kukruse Formation (L. Caradoc), Kohtla-Järve, Estonia, USSR. Fig. 144, brachial valve interior, BB 5149, $\times 5$; Fig. 145, pedicle valve interior, BB 5150, $\times 5$; Fig. 146, conjoined valves, BB 5147, $\times 5$;

Fig. 147, interior of pedicle valve, BB 5151, $\times 5$; Fig. 148, downward and lateral views of conjoined valves, BB 5148, $\times 3$.

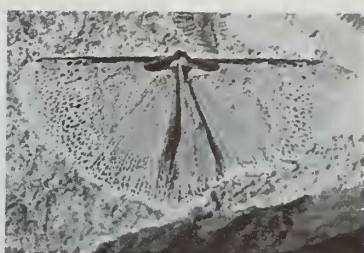
- Sowerbyella vulgata* Cooper, 1956: 801; pl. 198, figs 1–22; pl. 202, figs 16–23; pl. 206, figs 8–12 from Bromide Formation (U. Llandeilo), S. of Sulphur, Murray County, Oklahoma, USA.
- SPECIES QUESTIONABLY ASSIGNED
- Plectambonites aequistriatus* Willard, 1928: 276; pl. 3, figs 8, 9 from Ottosee Formation (L. Caradoc), Liberty Hill, Tennessee, USA (revised Cooper 1956: 775; pl. 197, figs 25–34, but no interiors figured).
- Plectambonites angulatus* Phleger, 1933: 18; pl. 1, fig. 1 from Barrel Spring Formation (Llandeilo–L. Caradoc), E. of Barrel Spring, Inyo Mountains, California, USA (no brachial interior figured).
- Sowerbyella (Sowerbyella) asperocostellata* Rozman, 1964: 155; pl. 11, figs 6–9 from Nalchan Formation (U. Ordovician), Kalychan River, Selenniyakh Mountains, NE USSR (no brachial interiors figured).
- Sowerbyella cava orientale* Oradovskaya, in Balashov *et al.* 1968: 49; pl. 47, figs 10–13 from L. Kharkindzhin Formation (Caradoc), River Inania, Omulev Mountains, NE USSR (no brachial interiors known).
- Plectambonites centricarinatus* Ruedemann, 1912: 92; pl. 4, fig. 7 from Indian Ladder Beds (Caradoc), Indian Ladder, Albany, New York, USA (no interiors figured).
- Plectambonites crassus* Willard, 1928: 278; pl. 3, fig. 10 from Holston Formation (L. Caradoc), McNutt Quarry, Sharon Springs, Virginia, USA (no interiors figured).
- Leptaena? detrita* Salter, in Salter & Blanford 1865: 30; pl. 3, fig. 6 from Llandeilo? beds, Kalajowar, Niti, India (no interiors known).
- Sowerbyella eha* Öpik, 1930: 158; pl. 9, fig. 122 from Kukruse Formation (L. Caradoc), Kohtla, Estonia, USSR (no brachial interiors figured).
- Leptaena geometrica* Kutorga, 1846: 104; pl. 4, fig. 3 from middle Ordovician beds, Pulkowa, near Leningrad, USSR (no interiors figured).
- Sowerbyella gigantea* Cooper, in Schuchert & Cooper 1930: 271; pl. 1, figs 19–20 from beds of Ashgill age, Percé, Québec, Canada (no information on denticles – might be *Eoplectodonta*).
- Plectambonites? kristiania* Høltedahl, 1916: 76; pl. 16, fig. 2 from 3cβ Beds (L. Llanvirn), Oslo City Centre, Norway (no interiors figured).
- Sowerbyella medioplicata* Cooper, 1956: 784; pl. 204, figs 1–5 from Upper Lincolnshire Formation (L.–M. Caradoc), Tumbling Run, Strasburg, Virginia, USA (no interiors figured).
- Sowerbyella merriami* Cooper, 1956: 785; pl. 269, figs 18–22 from shale below Eureka Quartzite (U. Llanvirn), Blair Ranch, Antelope Mountains, Nevada, USA (no interiors figured).
- Sowerbyella? minuta* Wilson, 1946: 50; pl. 3, fig. 23 from Cobourg Formation (U. Caradoc), Notre Dame Cemetery, Eastville, Ontario, Canada (no interiors figured).
- Sowerbyella minuta* Kulkov, 1967: 67; pl. 11, figs 7–9 from L. Chagyrskaya Formation (U. Llandovery), River Yarovski, Gornoi Altai, USSR (no brachial interior figured – n.b. this is an objective homonym of *S.? minuta* Wilson, 1946).
- Plectambonites negritus* Willard, 1928: 278; pl. 3, fig. 13 from Lenoir Formation (U. Llandeilo), Catawba Valley, N. of Salem, Virginia, USA (no interiors figured).
- Sowerbyella (Viruella) orechovensis* Nikanorova, 1976: 115; figs 1a–b from Tallinn Horizon (Llandeilo–L. Caradoc), Buiskayar, Orekovo, Moscow syncline, USSR (no brachial interior figured).
- Sowerbyella (Viruella?) orviku* Rõõmusoks, 1959: 15; pl. 1, figs 1, 2 from Uhaku Horizon (U. Llandeilo), Viyarke-Pakri, Estonia, USSR (no interiors figured).
- Sowerbyella patula* Öpik, 1930: 154; pl. 9, fig. 116 from Kukruse Formation (L. Caradoc), Kohtla, Estonia, USSR (no brachial interior figured).
- Sowerbyella (Sowerbyella) plana* Rõõmusoks, 1959: 26; pl. 4, figs 1–4 from Idavere Horizon (M. Caradoc), Aluvere, Estonia, USSR (no interiors figured).
- Sowerbyella (Sowerbyella) plana* Klenina, 1984: 80; pl. 7, figs 9, 13, 14, 16, 18 [name objectively preoccupied by *S. plana* Rõõmusoks] from Abaevskaya Formation (Llanvirn–Llandeilo), SE Ordatas Hill, NE Pre-Chinghiz Mountains, Kazakhstan, USSR (no interiors known).
- Sowerbyella plicatifera* Cooper, 1956: 791; pl. 203, figs 1–15 from Bromide Formation (U. Llandeilo), Decker's section, Nebo, Oklahoma, USA (no interiors figured).
- Leptaena praecosis* Sardeson, 1892: 329; pl. 4, figs 26–28 from Maquoketa Formation (Ashgill), Fillmore County, Minnesota, USA (no interiors known).
- Plectambonites quinquecostata* var. *depressa* Reed, 1917: 878; pl. 14, figs 18, 19 from Shalloch Formation (L. Ashgill), Shalloch Mill, Girvan, Scotland (no interiors figured).
- Sowerbyella quinquecostata estona* Öpik, 1930: 164; pl. 9, fig. 130 from Kukruse Formation (L. Caradoc), Kohtla, Estonia, USSR (no interiors figured).
- Leptaena repanda* Salter, in Salter & Blanford 1865: 29; pl. 3, fig. 3 from lower Ordovician beds, Damchen, Niti, NW India, and probable junior synonyms *Leptaena himalensis* and *L. himalensis* var. *textilis* Salter, in Salter & Blanford 1865: 28; pl. 3, figs 4, 5 from similar beds at Chorhoti Pass, Niti (no interiors known, but revised Reed 1912).
- Sowerbyella? rotunda* Rozman, 1964: 157; pl. 12, figs 1–5 from Nalchan Formation (U. Ordovician), Kalychan River, Selenniyakh Mountains, NE USSR (no brachial interiors figured).
- Leptaena schmidti* [Törnquist MS] Lindström, in Angelin & Lindström 1880: 29; pl. 14, figs 25, 26 from late Ordovician Beds, Boda, Sweden (no interiors figured).
- Sowerbyella rugosa triradiata* Butts, 1942: 113; pl. 96, fig. 9 from Oranda Formation (L. Caradoc), W. of Strasburg, Virginia, USA (no interiors figured).
- Sowerbyella silicica* Cooper, 1956: 793; pl. 196, figs 20–26 from Arline Formation (U. Llandeilo), Porterfield Quarry, Virginia, USA and subspecies *nana* Cooper, 1956: 794; pl. 196, figs 15–19, from same horizon and locality (no interiors figured).
- Sowerbyella subovalis* Wilson, 1932: 393; pl. 4, figs 10, 11 from L. Coburg formation (U. Caradoc), Cornwall, Ontario, Canada (no interiors figured).
- Orthis tenuissimestriata* M^cCoy, 1846: 35; pl. 3, fig. 20 from beds of Caradoc age, Slieve Roe, Co. Wicklow, Ireland (no interiors figured).
- Chonetes? hebavensis* Reed, 1906: 57; pl. 5, fig. 16 from Naungkangyi Beds (? L. Caradoc), Lebyaungbyan, Northern Shan States, Burma (no interiors known).
- Leptaena trabeata* Lindström, in Angelin & Lindström 1880: 30; pl. 17, figs 1–4 from Upper Ordovician Beds (?Fjäckå Shales), Västergötland, Sweden (no interiors figured).
- Sowerbyella undosa* Öpik, 1930: 159; pl. 21, figs 265–6 from Idavere Formation (L. Caradoc), Kohtla, Estonia, USSR (no interiors figured).



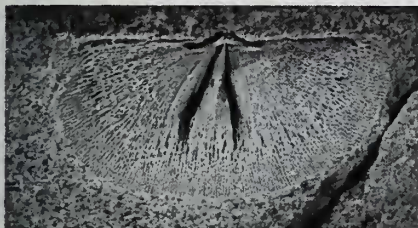
149



150



151a



152



151b

Figs 149–152 *Sowerbyella (Eochonetes) advena* Reed, 1917, from Starfish Bed, South Threave Formation (Ashgill: U. Rawtheyan), 650 m ENE of South Threave Farmhouse, Girvan, Strathclyde, Scotland. Fig. 149, natural internal mould of pedicle valve on the same slab as the lectotype, BC 10817, $\times 5$; Fig. 150, natural internal mould of pedicle valve, lectotype selected Cocks 1978: 100, the original of Reed 1917: pl. 21, fig. 6, B 73920, $\times 3$; Fig. 151a, downward view of natural internal mould of brachial valve and 151b, tilted obliquely to give an anterior view of the distinctive 'Thaerodonta' hinge line, BC 10291, $\times 3$ and $\times 5$; Fig. 152, interior of natural mould of brachial valve, the original of Reed 1917: pl. 21, fig. 11, B 73919, $\times 3$.

Sowerbyella wilsoni Reed, 1936: 41; pl. 4, figs 4–8 from Naungkangyi Formation (?L. Caradoc), Taung-bu, Southern Shan States, Burma (no brachial interior figured).

- 1967 *Thaerodonta* Havlíček: 58
- 1972 *Thaerodonta* Howe: 441
- 1974 *Thaerodonta* Amsden: 61
- 1974 *Eochonetes* Amsden: 61
- 1977 *Eoplectodonta* Mitchell: 89 *pars*
- 1981 *Thaerodonta* Rõõmusoks: 61

SPECIES REJECTED

Leptaena aspera James, 1874: 151 (citing as types the specimens figured by Meek 1873: pl. 5, figs 3f, 3g under *Leptaena sericea*) from the Cincinnati Group (L.–M. Caradoc), Ohio River, Cincinnati, Ohio (the illustrated specimens show a bilobed cardinal process, and the species appears to be an early davidsoniacean).

Sowerbyella ? austrum Öpik, 1953: 14; pl. 3, figs 17, 18 from Wapentake Formation (U. Llandovery), Heathcote, Victoria, Australia (to *Jonesea* gen. nov.)

Sowerbyella transversalis brevis Northrop, 1939: 176; pl. 15, figs 11–14 from Clemville Formation (L. Wenlock), Clemville, Gaspé, Québec, Canada (no interiors known, but shape almost certainly indicates *Leangella*).

Sowerbyella fasciola Yin, 1937: 288; pl. 1, fig. 10 from beds of probable Caradoc age, Shihtien, W. Yunnan Province, China (only brachial valve external known, but it looks like a strophomenacean).

Sowerbyella ? plebia Talent, 1965: 23; pl. 5, figs 6, 7 from McIvor Formation (Pridoli?), Redcastle, Victoria, Australia (to *Plectodonta (Plectodonta)*).

TYPE SPECIES. *Chonetes (Eochonetes) advena* Reed, 1917. Type species of *Thaerodonta* is *Thaerodonta aspera* Wang, 1949.

DIAGNOSIS. Like *Sowerbyella (Sowerbyella)* but with denticles on the brachial valve hinge line and opposing small sockets on the pedicle valve hinge line. Canals in pedicle valve hinge line variably developed, usually absent.

DISCUSSION. Close examination of topotype *Eochonetes advena* reveals the presence of denticles on the brachial valve hinge line (particularly laterally) and corresponding fossettes on the pedicle valve hinge line (Fig. 151). As discussed below, this is the only point of difference between *Thaerodonta* and *Sowerbyella*, and thus *Eochonetes* is placed here as a subgenus of *Sowerbyella*. Various plectambonitaceans, e.g. *Chonetoidea radiaula*, have perforated hinge lines in the same way as *Eochonetes* and we follow Jones (1928) in not considering this feature of generic or subgeneric importance, particularly since over half of the specimens in *Eochonetes* populations lack these canals. Since the original erection of *Thaerodonta* by Wang (1949) many authors have discussed the true generic characters and how the genus may best be separated from *Eoplectodonta*, *Sowerbyella*, *Viruella* and other closely related genera (e.g. Spjeldnaes 1957, Howe 1965, Williams 1965, Havlíček 1967, Cocks 1970, Macomber 1970, Howe 1972, Amsden 1974, Mitchell 1977, and Rõõmusoks 1981). Of all these papers, by far the best is Howe (1972) since he not only figures the hinge lines of the various genera very

SOWERBYELLA (EOCHONETES) Reed, 1917
Figs 149–152

- 1917 *Chonetes (Eochonetes)* Reed: 916
- 1928 *Sowerbyella* Jones: 474 *pars*
- 1949 *Thaerodonta* Wang: 19
- 1965 *Thaerodonta* Howe: 648
- 1965 *Eoplectodonta* Williams: H380 *pars*
- 1965 *Eochonetes* Williams: H380



153



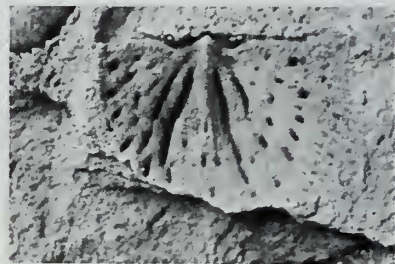
154



155a



155b



156

Figs 153–156 *Plectodonta mariae* Kozłowski, 1929, from Taina Formation, Borshchov Group (Lochkovian), Figs 153, 155 from river bank at Krzywcz, Figs 154, 156 from Rukhotin Valley in Rukhotin Village, both Podolia, Ukraine, USSR. Fig. 153, brachial valve interior, B 81372, $\times 6$; Fig. 154, natural internal mould of brachial valve, BB 65810, $\times 11$; Fig. 155, dorsal and ventral views of a pair of conjoined valves, B 81371, $\times 4.5$; Fig. 156, natural internal mould of brachial valve, BB 65811, $\times 11$.



Fig. 157 *Plectodonta mariae* Kozłowski, 1929, internal mould of brachial valve, from Taina Formation (Lochkovian), Rukhotin, Podolia, Ukraine, USSR (based on BB 65810), $\times 12$.

well, but also discusses their various characters. We follow Wang and Howe in accepting the nature of the denticles on the hinge line as the fundamental difference between *Thaerodonta* and *Eoplectodonta* – in the former the protuberances are all on the brachial valve and the pits all on the pedicle valve, whilst in *Eoplectodonta* the denticles are on the pedicle valve and the pits on the brachial valve. In some species and specimens of *Thaerodonta* the denticles are confined to the lateral parts of the hinge line, in contrast to *Eoplectodonta* in which some species only have denticles in the centre, near the teeth. However, again following Howe (1972), apart from the presence of denticles we can find no consistent differences between *Thaerodonta* and *Sowerbyella* and thus we treat *Thaerodonta* as a subgenus of *Sowerbyella* here. However, in a few species attributed to *Sowerbyella* by Howe, such as '*S. rugosa*', because of the partial denticulation we prefer to refer them to *Eochonetes*. Various authors have found differences between *Sowerbyella* and *Thaerodonta* in their side septa; however, there is so much variation in *Sowerbyella* that we cannot use these features to separate the two subgenera.

Some authors, e.g. Wang (1949) and Howe (1972), have argued that there are strongly developed accessory teeth and delthyrial thickening in *Thaerodonta* which distinguish it from *Eochonetes*, but we can find no substantial differences between them. Therefore *Eochonetes* is now established as a senior synonym of *Thaerodonta*.

SPECIES ASSIGNED

Chonetes (Eochonetes) advena Reed, 1917: 915; pl. 21, figs 6–11 from Drummock Group (M. Ashgill), Thraive Glen, Girvan, Scotland.

Thaerodonta aspera Wang, 1949: 20; pl. 11, figs 1–5 from Elgin Member of Maquoketa Formation (L. Ashgill), Orleans, Iowa, USA.

Eochonetes canaliferus Havlíček, 1971: 69; pl. 20, figs 12, 13 from U. Ktaoua Formation (Ashgill), Jbel Mimount, Maïdere, Morocco.

Eochonetes celticus Mitchell, 1977: 88; pl. 17, figs 20–25 from Junction Beds (Caradoc–Ashgill), Pomeroy, Co. Tyrone, Northern Ireland.

Thaerodonta convexa Rõõmusoks, 1981: 67; pl. 2, figs 1–5 from Kõrgessaare Formation (L. Ashgill), Paopa, Estonia, USSR.

Thaerodonta dignata Wang, 1949: 22; pl. 11, figs 1–6 from L. Maquoketa shale (L. Ashgill), Clermont, Iowa, USA.

Thaerodonta johnsonella Amsden, 1974: 60; pl. 23, figs 3a–e; pl. 24, figs 1a–u from Leemon Formation (U. Ashgill), Blue Shawnee Creek, Cape Girardeau County, Missouri, USA.

Thaerodonta magna Howe, 1965: 651; pl. 82, figs 1–7 from Aleman Limestone (L. Ashgill), Hueco Mountains, Texas, USA.

Thaerodonta moelsi Rõõmusoks, 1981: 66; pl. 1, figs 6–11 from Kõrgessaare Formation, (L. Ashgill), Kõrgessaare, Estonia, USSR.

Thaerodonta mucronata Howe, 1965: 648; pl. 81, figs 18–29 from Aleman Limestone (L. Ashgill), Trans-Pecos, Texas, USA (and subspecies *scabra* Howe, 1965: 648; pl. 82, figs 9–11, also from the Aleman Limestone)

Plectambonites rugosus noquettensis Hussey, 1926: 160; pl. 7, fig. 6 from Ogontz Member of Stonington Formation (Caradoc–Ashgill), east of Church, Michigan, USA.

Thaerodonta nubila Rõõmusoks, 1981: 68; pl. 2, figs 6–10 from Adila Formation (U. Ashgill), Kaapsalyski Cliff, Estonia, USSR.

Leptaena recedens Sardeson, 1892: 330; pl. 4, figs 29–32 from Cincinnati Group (L. Ashgill), Spring Valley, Fillmore County, Minnesota, USA (revised Wang 1949: 20; pl. 11, figs 1–3 and Howe 1988: 214; figs 2.9–2.12, 2.14–2.17, 10, 11).

Plectambonites rugosa-clarksvillensis Foerste, 1912: 127; pl. 1, figs 7a–c; pl. 10, figs 7a–d from the Richmond Group (L. Ashgill), Oxford, Ohio, USA (revised Howe 1972: 445; pl. 1, figs 1–3 and Howe 1979: 4; pl. 2, figs 14–17 and placed in synonymy of *Thaerodonta recedens* by Howe 1988: 214).

Thaerodonta saunjaensis Rõõmusoks, 1981: 65; pl. 1, figs 1–5 from Saunja Member of Voore Formation (L. Ashgill), Miaremetsa, Estonia, USSR.

Leptaena saxea Sardeson 1892: 330; pl. 4, figs 33–35 from Cincinnati Group (L. Ashgill), Bristol, Fillmore County, Minnesota, USA (revised Wang 1949: 21; pl. 11, figs 1–5).

SPECIES QUESTIONABLY ASSIGNED

Plectambonites glabra Shaler, 1865: 64 from Ellis Bay Formation (M.–U. Ashgill), Anticosti Island, Quebec, Canada (revised by Twenhofel (1928: 190) as *P. sericeus* var. *glaber*, but unfigured; probably a *Sowerbyella* but true subgenus unknown).

SOWERBYELLA (RUGOSOWERBYELLA) Mitchell, 1977

977 *Sowerbyella* (*Rugosowerbyella*) Mitchell: 83

TYPE SPECIES. *Plectambonites subcorrugatella* Reed, 1917, a subjective senior synonym of *Ptychoglyptus ambiguus* Reed, 1952.

DIAGNOSIS. Like *Sowerbyella* (*Sowerbyella*) but with concentric rugae truncated and offset by accentuated costae.

REMARKS. Mitchell's figures (1977: pl. 16, figs 31, 32) again call attention to the fact that a median septum is sometimes present and sometimes absent within a single population of *Sowerbyella*, and this feature cannot be used as a generic character. Of the two specimens of *S. (R.) insueta* figured by Klenina (1984: pl. 8) only the holotype (fig. 19) has concentric rugae over the whole valve: the other specimen (fig. 18) has strong posterolateral rugae but these are not developed in the central part of the valve.

SPECIES ASSIGNED

Plectambonites subcorrugatella Reed, 1917: 886; pl. 15, figs 33, 34 from Whitehouse Group (L. Ashgill), Shalloch Mill, Girvan, Scotland, a senior synonym of *Ptychoglyptus shallochensis* Reed, 1935: 7; pl. 1, fig. 5 from the same horizon and locality, *Ptychoglyptus ambiguus* Reed 1952: 56; pl. 2, figs 15, 16 from the Killey Bridge Formation (L. Ashgill), Killey Bridge, Pomeroy, Co. Tyrone, Northern Ireland and *Sowerbyella foveata* Reed, 1952: 52; pl. 2, fig. 11 from the same horizon and locality (all revised Mitchell 1977: 83; pl. 16, figs 23–27).

SPECIES QUESTIONABLY ASSIGNED

Sowerbyella bellarugosa Ulrich & Cooper, 1938: 186; pl. 38, figs 1–3 from Antelope Valley Formation (U. Llanvirn), Ikes Canyon, Nevada, USA (certainly rugose and a *Sowerbyella*; uncertainly assigned to this subgenus).

Sowerbyella (Viruella) praestans Klenina, in Klenina *et al.* 1984: 83; pl. 8, figs 18, 19 from Babanskaya Formation (Caradoc), SW Pre-Chinghiz Mountains, Kazakhstan, USSR (certainly rugose and a *Sowerbyella*; uncertainly assigned to this subgenus).

Sowerbyella ? rosettana Henningsmoen, 1948: 396; pl. 24, figs 9–12 from Red Tretaspis Mudstone (L. Ashgill), Jonstorp, Västergötland, Sweden (certainly rugose and a *Sowerbyella*; no interiors illustrated).

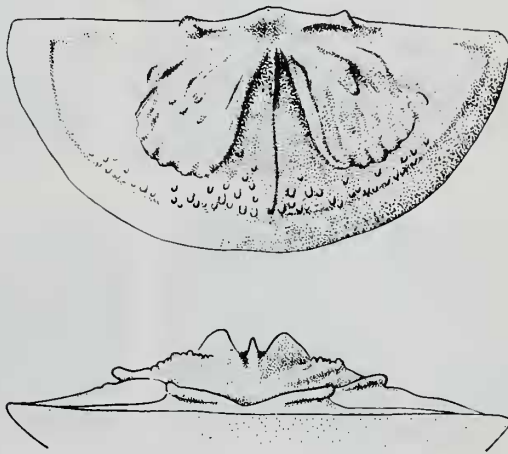


Fig. 158 *Cooperia siphonata* (Cooper, 1956), interior views of the brachial valve, from Pratt Ferry Formation (Llandeilo), Pratt Ferry, Alabama, USA (based on BC 10305), $\times 15$.

Subfamily CRASPEDELIINAE subfam. nov.

DIAGNOSIS. Bema divided. Cardinal process undifferentiated (i.e. present but fused and indivisible laterally from its surrounding structures, see Fig. 158).

GENERA ASSIGNED. *Craspedelia* Cooper, 1956; *Cooperia* gen. nov.

RANGE. Llandeilo (*Craspedelia marginata*) to M. Caradoc (*Craspedelia gabata*).

REMARKS. This new subfamily differs from the other two within the family in having an undifferentiated cardinal process, which we feel warrants separation at subfamilial level. It differs from the Ptychoglyptinae in its divided bema.

CRASPEDELIA Cooper, 1956

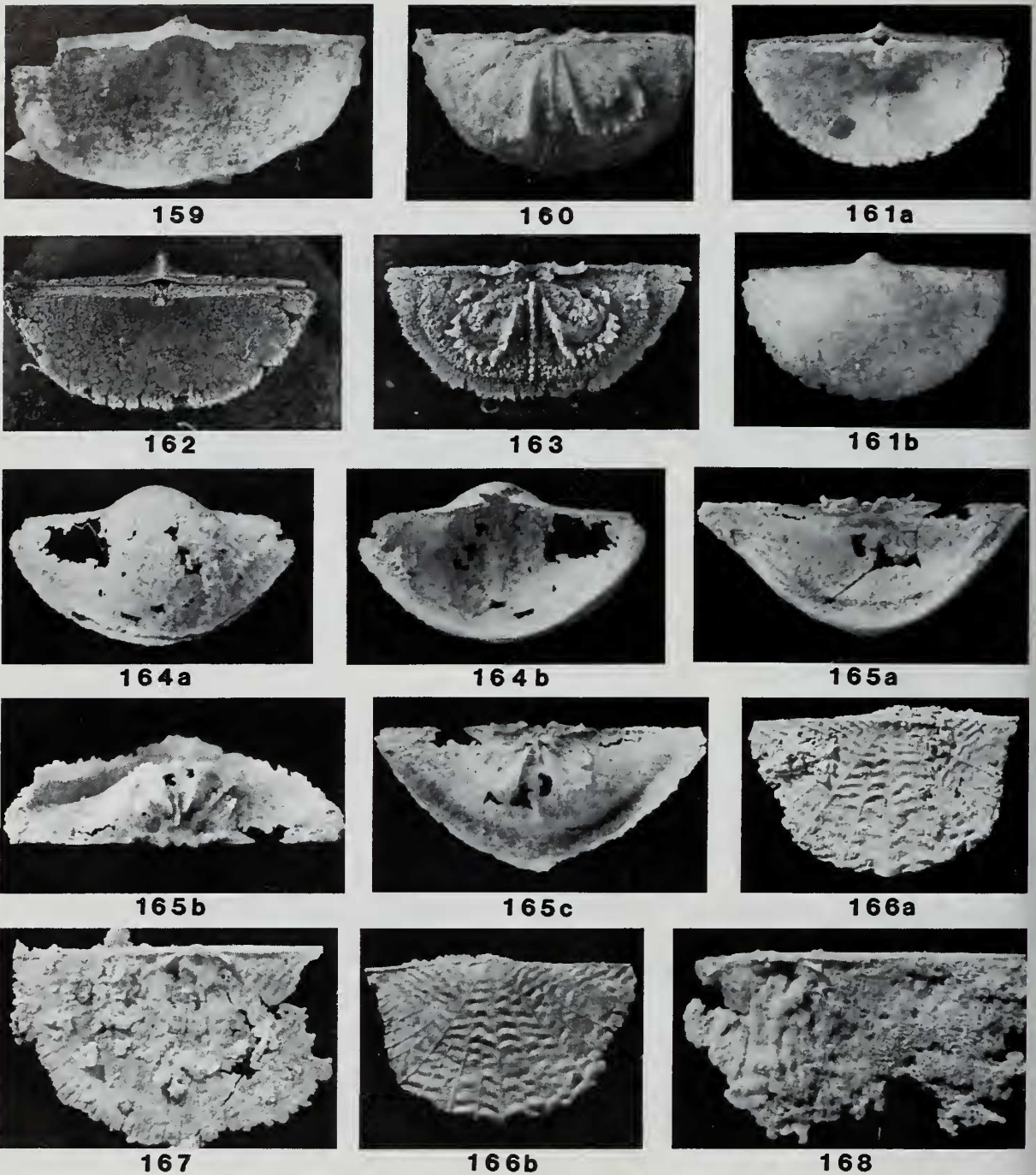
Figs 164, 165

1956 *Craspedelia* Cooper: 772

1965 *Craspedelia* Williams: H383

TYPE SPECIES. *Craspedelia marginata* Cooper, 1956.

DIAGNOSIS. As for subfamily. Geniculate with additional anterior deflection and with a fold and sulcus. No ornament known.



Figs 159–163 *Cooperea siphonata* (Cooper, 1956) gen. nov., from Pratt Ferry Formation (Llandeilo), SE of Pratt Ferry, Blocton, Alabama, USA. Fig. 159, interior of pedicle valve, BC 10303, $\times 10$; Fig. 160, interior of brachial valve, BC 10305, $\times 10$; Fig. 161, dorsal and ventral views of a pair of conjoined valves, BC 10302, $\times 10$; Fig. 162, pair of conjoined valves, holotype, the original of Cooper 1956: pl. 210, figs 17, 18, 21, 22, USNM 117470a, $\times 10$; Fig. 163, interior of brachial valve, the original of Cooper 1956: pl. 210, figs 23, 24, USNM 117470e, $\times 10$

Figs 164, 165 *Craspedelia marginata* Cooper, 1956, from Pratt Ferry Formation (Llandeilo), SE of Pratt Ferry, Blocton, Alabama, USA. Fig. 164, external and internal views of a pedicle valve, BC 7300, $\times 8$; Fig. 165, external, posterior and internal views of a brachial valve, BC 7301, $\times 8$.

Figs 166–168 *Ptychoglyptus virginienensis* Willard, 1928, from Pratt Ferry Formation (Llandeilo), SE of Pratt Ferry, Blocton, Alabama, USA. Fig. 166, dorsal and ventral views of a pair of conjoined valves, BC 10317, $\times 3$; Fig. 167, brachial valve interior, BC 10316, $\times 3.5$; Fig. 168, brachial valve interior, BC 10318, $\times 7$.

REMARKS. *Craspedelia* has previously been assigned to the *Bimuriidae*, but that family has a simple cardinal process whilst the cardinal process of *Craspedelia* is undoubtedly undercut. The geniculation is very distinctive, buckling both ways and paralleled in the Plectambonitacea only by *Leinversella*.

SPECIES ASSIGNED

Craspedelia gabata Williams, 1962: 179; pl. 17, figs 11, 12, 16, 17 from lower Ardwell Greywackes (M. Caradoc), Pinmore, Girvan, Scotland.

Craspedelia marginata Cooper, 1956: 773; pl. 213, figs 1–20 from Pratt Ferry Formation (Llandeilo), Pratt Ferry, Alabama, USA.

Craspedelia tata Popov, 1980a: 55; pl. 17, figs 6–9 from Erkebidaiski Horizon (M. Ordovician), Tselinogradsk, N. Kazakhstan, USSR.

SPECIES QUESTIONABLY ASSIGNED

Craspedelia sp. of Nikitin & Popov 1984: 151; pl. 18, figs 3, 4 from Sargaldakskaya Formation (U. Caradoc), Sargaldak River, Chinghiz Mountains, Kazakhstan, USSR (no interiors known).

COOPEREA gen. nov.

Figs 158–163

TYPE SPECIES. *Bimuria siphonata* Cooper, 1956. Named after Dr G.A. Cooper.

DIAGNOSIS. Like *Craspedelia* but with no geniculation.

REMARKS. The species assigned to *Bimuria* by Cooper (1956) can be divided into two groups, the first, including the type species *B. superba*, has a simple cardinal process, but the second group, consisting of *B. siphonata* and *B. immatura*, has an undercut cardinal process and so can be put into a different family, the Sowerbyellidae. The new genus is close to *Craspedelia* in morphology, but in very many specimens lacks any sign of geniculation or other deviation from normal plectambonitacean convexity. *C. siphonata* is common in the Pratt Ferry Formation; Dr G. A. Cooper very kindly allowed one of us (L.R.M.C.) to pick over briefly some duplicate residues and there are now over 80 valves in the British Museum (Natural History) registered (including BC 7289–99). In none of the brachial valves available to us or to Cooper (1956: 770) is a cardinal process preserved; this may however be owing to the lack of silicification of the very thin sheet-like cardinal process which we think may have been present between the robust socket plates.

SPECIES ASSIGNED

Bimuria immatura Cooper, 1956: 776; pl. 211, figs 1–13 from Effna–Rich Valley Formation (L. Caradoc), Porterfield Quarry, Virginia, USA.

Bimuria siphonata Cooper, 1956: 770; pl. 210, figs 17–24 from Pratt Ferry Formation (Llandeilo), Pratt Ferry, Alabama, USA.

Subfamily **PTYCHOGLYPTINAE** Cooper, 1956

1956 Ptychoglyptinae Cooper: 815

1965 Ptychoglyptinae Williams: H381

DIAGNOSIS. Weak bema not divided. Cardinal process differentiated.

REMARKS. The very distinctive ornament of *Ptychoglyptus* can only be regarded as a generic character, nevertheless the genus stands on its own in view of the unique combination of possessing an undivided bema, side septa and undercut cardinal process. Cooper (1956: 815) erected the subfamily on the 'poorly developed septa in the brachial valve' as opposed to the Sowerbyellinae, but they are present in some *Ptychoglyptus* and we prefer to separate the subfamily on the undivided bema.

GENUS INCLUDED. *Ptychoglyptus* Willard, 1928.

RANGE. L.–U. Caradoc.

PTYCHOGLYPTUS Willard, 1928

Figs 166–168

1928 *Ptychoglyptus* Willard: 283

1956 *Ptychoglyptus* Cooper: 815

1965 *Ptychoglyptus* Williams: H381

TYPE SPECIES. *Ptychoglyptus virginienensis* Willard, 1928.

DIAGNOSIS. Ornament of small rugae interrupted by costellae.

REMARKS. The bema and side septa are not developed in most members of the population; nevertheless, when they are seen in gerontic specimens the bema can be seen to be undivided.

SPECIES ASSIGNED

Ptychoglyptus virginienensis var. *irregularis* Reed, 1941: 274; pl. 5, fig. 8 from Balclatchie Beds (L. Caradoc), Balclatchie, Girvan, Scotland.

Ptychoglyptus virginensis [sic] *mendocina* Levy & Nullo, 1975: 27; pl. 1, figs 1–5 from L. Caradoc beds, Ponon-Trehué, Mendoza, Argentina.

Ptychoglyptus valdari Spjeldnaes, 1957: 58; pl. 1, figs 1–3 from Zone 4ba (M. Caradoc), Slependen, Oslo, Norway.

Ptychoglyptus virginienensis Willard, 1928: 283; pl. 2, fig. 12 from Eifna Formation (L. Caradoc), McNutt Quarry, Bland, Virginia, USA.

SPECIES QUESTIONABLY ASSIGNED

Ptychoglyptus bellarugosus Cooper, in Schuchert & Cooper 1930: 269; pl. 1, fig. 5 from U. Ashgill Beds, Priest's Road, Percé, Québec, Canada (no interiors known).

Ptychoglyptus geniculatus Oradovskaya, in Balashov *et al.* 1968: 50; pl. 47, figs 1–5 from Kharkindzhin Formation (Caradoc), Inaniya River, Omulev Mountains, NE USSR (no interiors illustrated).

Ptychoglyptus ? *kindlei* Cooper, 1956: 816; pl. 172, figs 7–12 from boulder in Mystic Conglomerate (Llandeilo–Caradoc), Stanbridge, Québec, Canada (no interiors known).

Ptychoglyptus ? *matura* Cooper, 1956: 817; pl. 174, figs 5, 6 from Pratt Ferry Formation (Llandeilo), Pratt Ferry, Alabama (no interiors known).

Ptychoglyptus pauciradiatus Reed, 1932a: 122; pl. 18, figs 1, 2 from Hovin Sandstone (Caradoc), Grimsåsen, Trondheim, Norway (no interiors illustrated).

Rafinesquina ? *ringerikiensis* Holtedahl, 1916: 30; pl. 3, fig. 7 from Zone 4b (M.–U. Caradoc), Bratterud, Ringerike, Norway (no interiors known).

Ptychoglyptus shanensis Reed, 1932b: 195; pl. 3, fig. 15 from Pindaya Formation (Caradoc?), Yeosin, Southern Shan States, Burma (no interiors known).

Ptychoglyptus ulrichi Endo, 1932: 46; pl. 35, figs 1–6 from

Middle Ordovician beds, Huang-pa-yi, Shaanxi Province, China (no interiors known).

Ptychoglyptus 'ex gr. *virginiensis*' of Rozman 1981: 138; pl. 31, figs 1–3 from *Christiania subquadrata* beds (Llandeilo), Agach-Ula, W. Mongolia (no interiors known).

Ptychoglyptus sp. of Klenina 1984: 86; pl. 8, fig. 17 from Sargaldakskaya Formation (U. Caradoc), NE Prechinhiz Hills, Kazakhstan, USSR (no interiors known).

Ptychoglyptus sp. of Nikitin & Popov 1984: 150; pl. 18, figs 1, 2 from Sargaldakskaya Formation (U. Caradoc), Sargaldak River, Chinghiz Mountains, Kazakhstan, USSR (no interiors known).

SPECIES REJECTED

Ptychoglyptus ambiguus Reed, 1952: 56; pl. 2, figs 15, 16 from Killey Bridge Formation (L. Ashgill), Killey Bridge, Pomeroy, Northern Ireland (junior synonym of *Rugosowerbyella subcorrugata*).

Ptychoglyptus shallochensis Reed, 1935: 7; pl. 1, fig. 5 from Whitehouse Group (L. Ashgill), Shalloch Mill, Girvan, Scotland (junior synonym of *Rugosowerbyella subcorrugata*).

Ptychoglyptus ulrichi Endo, *sensu* Fu 1982: 118; pl. 36, fig. 1 from Xiliangsi Formation (Arenig–Llanvirn), Liangshan, Nanzheng County, S. Shaanxi, China (wrong ornament for *Ptychoglyptus*, no interior known, superfamily uncertain).

PLECTAMBONITACEAN GENERA UNASSIGNED TO FAMILIES

It is probable that *Goniotrema*, *Leptoptilum*, *Nabiaioia*, *Paucicostella*, *Pseudoanisopeurella* and *Ukoa* are all plectambonitaceans, but they cannot yet be assigned to any family with confidence, largely because the published material is inadequate.

GONIOTREMA Ulrich & Cooper, 1936

- 1936 *Goniotrema* Ulrich & Cooper: 626
 1938 *Goniotrema* Ulrich & Cooper: 193
 1956 *Goniotrema* Cooper: 711
 1965 *Goniotrema* Williams: H373

TYPE SPECIES. *Goniotrema perplexum* Ulrich & Cooper, 1936.

DISCUSSION. Only a single specimen of the genus has ever been found, although both valves are present and they are now disarticulated. The cardinal process is not undercut but may not be completely preserved (Cooper 1956: 711) and the correct systematic position of the genus remains unknown. There is no bema and no side septa, although a weak platform is developed, and the genus may perhaps be a leptellinid.

SPECIES ASSIGNED

Goniotrema perplexum Ulrich & Cooper, 1936: 626 (illustrated Ulrich & Cooper 1938: pl. 40, figs 23–28) from U. Pogonip Group (Llanvirn), Ikes Canyon, Nevada, USA.

LEPTOPTILUM Öpik, 1930

- 1930 *Leptestia* (*Leptoptilum*) Öpik: 130
 1960 *Leptoptilum* Sokolskaya: 208

1965 *Leptestia* Williams: H373 *pars*

TYPE SPECIES. *Leptestia* (*Leptoptilum*) *bekkeri* Öpik, 1930.

DISCUSSION. Öpik (1930: pl. 7, fig. 81) only figured a broken fragment of pedicle valve interior and another broken pedicle valve exterior upon which no generically diagnostic characters can be seen. Until the type species is properly revised from topotype specimens the genus should remain of doubtful validity. Öpik distinguished his new subgenus on the basis of distinctive transverse sculpture, but this cannot be seen clearly in his illustration.

SPECIES ASSIGNED

Leptestia (*Leptoptilum*) *bekkeri* Öpik, 1930: 131; pl. 7, fig. 81 from Kukruse Formation (L. Caradoc), Kohtla, Estonia, USSR.

SPECIES QUESTIONABLY ASSIGNED

Plectambonites transversum Pander, 1830 from U. Arenig–Llandeilo, south of Leningrad, USSR (assigned to *Leptoptilum* by Sokolskaya 1960: pl. 27, fig. 16, but no interior figured).

NABIAOIA Xu, 1979

1979 *Nabiaioia* Xu: 370

TYPE SPECIES. *Nabiaioia pusilla* Xu, 1979.

DISCUSSION. Only two brachial valves and no pedicle valve are known of this genus. They are small (width 4.2 mm and length 2.3 mm) and the structures do not appear well developed in the interiors. Although it is possible that these Lower Devonian specimens are plectambonitaceans, they might in fact be chonetaceans or even pholidostrophiids.

SPECIES ASSIGNED

Nabiaioia pusilla Xu, 1979: 371; pl. 2, figs 18–20 from Tangxiang Formation (Eifelian), Luofu of Nandan, Guangxi Province, China.

PAUCICOSTELLA Cooper, 1956

- 1956 *Paucicostella* Cooper: 711
 1965 *Paucicostella* Williams: H373

TYPE SPECIES. *Paucicostella canadensis* Cooper, 1956.

DISCUSSION. Although Cooper (1956: 711) described the interior of this genus in generalized terms (as seen by wetting the exteriors), only the exteriors are figured, and until internal views are available the familial assignment and true status of this genus must remain doubtful.

SPECIES ASSIGNED

Paucicostella canadensis Cooper, 1956: 712; pl. 172, figs 1–6; pl. 173, fig. 24 from boulder in Mystic Conglomerate (Arenig–Llanvirn), Mystic, Québec, Canada.

PSEUDOANISOPEURELLA Xu, 1978

1978 *Pseudoanisopeurella* Xu, in Wang & Yan: 222

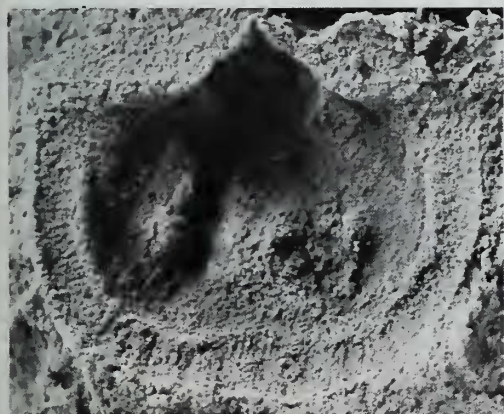
TYPE SPECIES. *Pseudoanisopeurella aetheta* Xu, 1978.



169a



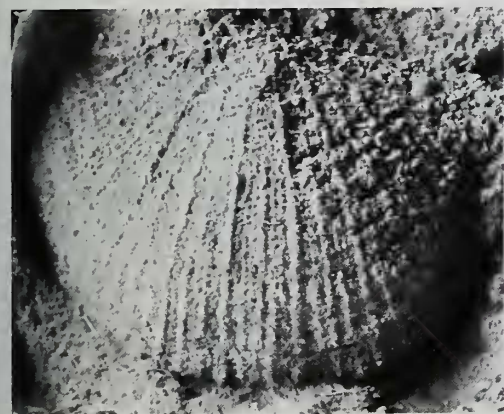
170



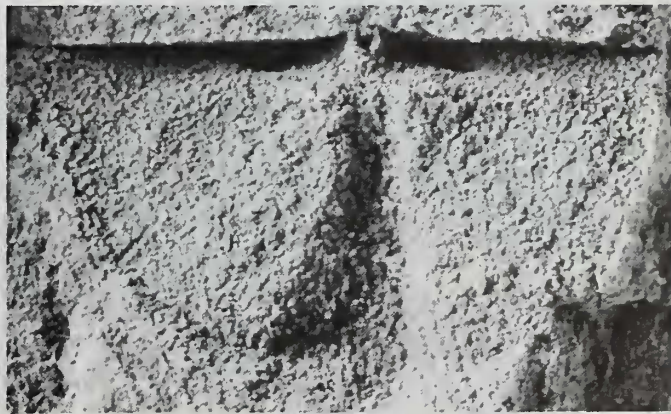
169b



171a



172



171b

Figs 169–172 *Kozhuchinella mariinica* Severgina, 1967, from Algan Formation (Tremadoc), River Poperechnaya, Kuznetz Alatau, Altai Mountains, USSR. Fig. 169, natural internal mould and latex cast of pedicle valve, the original of Severgina 1967: pl. 5, fig. 6, VSEGEI 422/1323, $\times 9$; Fig. 170, natural internal mould of pedicle valve, holotype, the original of Severgina 1967: pl. 5, figs 4, 4A, VSEGEI 420/1323, $\times 7.5$; Fig. 171, latex cast and natural internal mould of a brachial valve, the original of Severgina 1967: pl. 5, fig. 5, VSEGEI 423/1323, $\times 10$; Fig. 172, latex cast of external mould of a pedicle valve, the original of Severgina 1967: pl. 5, fig. 7, VSEGEI 421/1323, $\times 7$.



173a



173b



174



173c

Figs 173, 174 *Murjukiana ilovata* Severgina, 1967, from Ilovatski Horizon (L.-M. Ordovician), Suresov, Kuznetz Alatau, Altai Mountains, USSR. Fig. 173, latex casts of interior and exterior and natural internal mould of interior of a brachial valve, the original of Severgina 1967: pl. 5, figs 12, 13, VSEGEI 430-1/1323, $\times 3$; Fig. 174, natural internal mould of a pedicle valve, holotype, the original of Severgina 1967: pl. 5, fig. 11, VSEGEI 428/1323, $\times 4$.

DISCUSSION. Only the exterior of a pedicle valve is figured by Wang & Yan (1978: pl. 54, fig. 20) and no internals are known; the genus can be considered a *nomen dubium*.

SPECIES ASSIGNED

Pseudoanisopeurella aletheta Xu, in Wang & Yen 1978: 222; pl. 54, fig. 20 from U. Miaopo Formation (L. Caradoc), Fenxiang, Yichang County, W. Hubei Province, China.

UKOA Öpik, 1932

1932 *Ukoa* Öpik: 33
1965 *Ukoa* Williams: H372

TYPE SPECIES. *Ukoa ornata* Öpik, 1932.

DISCUSSION. Although Williams (1965: H272) states the shell is impunctate, the close-up view of a part of the ornament and adjacent shell figured by Öpik (1932: pl. 8, fig. 35) suggests to us that the type species possesses pseudopunctae and is properly classified within the Strophomenida. The type species is resupinate and weakly geniculate and may be related to *Inversella* and *Ahtiella*, but the interior is unknown and thus the genus cannot be accurately classified in this paper.

SPECIES ASSIGNED

Ukoa ornata Öpik, 1932: 33; pl. 4, figs 26-28; pl. 8, fig. 35 from Aseri Formation (Llanvirn), Tsitri, Estonia, USSR.

GENERA REJECTED FROM THE PLECTAMBONITACEA

The following genera have all been attributed to the Plectambonitacea by their original authors, but we do not consider them as forming part of the superfamily.

EOCRAMATIA Williams, 1974

1974 *Eocramatia* Williams: 128

TYPE SPECIES. *Eocramatia dissimulata* Williams, 1974.

DISCUSSION. The only known specimens of *Eocramatia* are of internal and external moulds, and, although we agree with Williams (1974: 128) that no traces of pseudopunctae are seen, a final decision on this point must await the discovery of

calcite shells. The cardinal process is undoubtedly bilobed and extending posteriorly from the hinge line, and with a pseudodeltidium and other features of the interarea so similar to *Gacella* and *Fardenia*, we place this genus within the Davidsoniacea.

SPECIES ASSIGNED

Eocramatia dissimulata Williams, 1974: 129; pl. 21, figs 9, 12, 14, 15; pl. 22, figs 1–3, 5, 6 from Hope Shales (L. Llanvirn), Brithdir, Shelve District, Shropshire, England.

KOZHUCHINELLA Severgina, 1967
Figs 169–172

1967 *Kozhuchinella* Severgina: 131
1984b *Kozhuchinella* Severgina: 48

TYPE SPECIES. *Kozhuchinella mariinica* Severgina, 1967.

DISCUSSION. The cardinal process is 'rudimental' (Severgina 1967). No shell material is preserved and thus its plectambonitacean affinities are not proven. The general form of the hinge, muscle fields and pallial markings indicate to us that placement within the Billingsellacea appears to be more appropriate. The original specimens are re-illustrated here.

SPECIES ASSIGNED

Kozhuchinella mariinica Severgina, 1967: 132; pl. 5, figs 4–7 from Algainski Horizon (Tremadoc), Poperechnaya River, Kusnetz-Altai, USSR.

MURJUKIANA Severgina, 1967
Figs 173, 174

1967 *Murjukiana* Severgina: 134

TYPE SPECIES. *Murjukiana ilovata* Severgina, 1967.

DISCUSSION. We are fortunate in being able to revise this genus from Severgina's original specimens, which consist of a brachial valve (both internal and external moulds) and a pedicle valve internal mould, all reillustrated here. In addition there are two incomplete pedicle valve internal moulds on the same slab as the brachial valve. There are no traces of pseudopunctae on any of the valve surfaces (although of course there is no original shell material remaining) and the genus does not come close to any known plectambonitacean morphology. The general form and shape of the valves, with a normally convex pedicle valve and a more or less flat brachial valve, coupled with well-defined interareas on both valves, indicate to us that the genus is probably an orthacean. The precise details of the cardinal process are slightly obscure, but it appears to consist of a simple small knob which is connected anteriorly to a shallow myophragm which extends approximately half the valve length. Although the delthyrium seems open, there appear to be some small chilidial plates. Its precise relationships to other contemporary orthaceans remain uncertain, but its affinities might lie within the Hesperonomiidae or Orthidae.

SPECIES ASSIGNED

Murjukiana ilovata Severgina, 1967: 135; pl. 5, figs 11–13 from Ilovatski Formation (Llanvirn), Kuznetz Alatau, Altai-Sayan, USSR.

OTTADALENITES Harper, 1981

1981 *Ottadalenites* Harper, in Bruton & Harper: 165

TYPE SPECIES. *Ottadalenites incertus* Harper, 1981.

DISCUSSION. Only internal and external moulds of this monospecific genus are known and thus there is no proof of pseudopunctate shell structure. The cardinalia and above all the style of ornamentation seem to be very similar to those of contemporary orthids, and we find no reason for assigning this genus to the Plectambonitacea. It is also poorly preserved and based on few specimens, and may best be treated as a *nomen dubium*.

SPECIES ASSIGNED

Ottadalenites incertus Harper, in Bruton & Harper 1981: 165; pl. 3, figs 1–6 from Otta Conglomerate (L. Llanvirn), Otta, Norway.

UJUKITES Andreeva, 1985

1985 *Ujukites* Andreeva: 41

TYPE SPECIES. *Ujukites altaicus* Andreeva, 1985.

DISCUSSION. Although interiors of this genus are figured, they do not show the cardinal process, and this is not mentioned in the text. The general internal and external form of the type species suggest that it may be better classified within the Strophomenacea rather than the Leptestiinae where the author placed it.

SPECIES ASSIGNED

Ujukites altaicus Andreeva, 1985: 41; pl. 4, figs 7–12, 15 from Stretinski? Formation (M. Ordovician), River Tuloi, Altai Mountains, USSR.

SPECIES QUESTIONABLY ASSIGNED

Ujukites tarlykensis Andreeva, 1985: 41; pl. 4, figs 13, 14, 16–19 from Tarliski Formation (M. Ordovician), River Ujuk, Tuva, USSR.

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¹ This title means 'Geological Bureau of Hubei Province' – no authors were named in it.

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